MERLEWOOD RESEARCH AND DEVELOPMENT PAPER

Number 53

A COMPARISON OF THE GROWTH OF TUNDRA PLANT SPECIES AT SEVERAL WIDELY SEPARATED SITES

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R. & D. 73/53

December 1973

A comparison of the Growth of Tundra Plant Species at Several Widely Separated Sites

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The data in this report will form the basis of a chapter dealing with the international synthesis of the growth of individual tundra species, to be presented at the final IBP Tundra Biome Meeting at Abisko, Sweden in 1974. In its final form, at present being prepared by the author and Nigel Collins, the chapter will include comparative data on graminoids and mosses. The present report is to circulate data obtained so far for liaison with other working groups within the primary production section of the Tundra Biome. Information contained herein should not be quoted without permission of the author.

The work described within this report was made possible through the provision of a visiting research fellowship awarded by The Royal Society, London, England.

CONTENTS

A COMPARISON OF THE GROWTH OF TUNDRA PLANT SPECIES AT SEVERAL WIDELY SEPARATED SITES

by

Terence V. Callaghan*

ABSTRACT

Part of a provisional synthesis of the growth of individual tundra plant species at a number of international sites is presented in this report. The processes of growth and population dynamics underlying biomass and primary production of a forb and several dwarf shrubs are described and compared between different habitats and between different national sites. Brief reference is made to graminoids and bryophytes which will be included in the final synthesis.

The life cycles of Polygonum viviparum and several tundra dwarf shrubs are outlined. In Polygonum viviparum, dry weight changes of plant components on an individual plant basis are followed throughout the growing season. Maximum seasonal plant dry weight is shown to be associated with site favourability, Niwot Ridge showing the highest values and Barrow meadow the lowest values. Biomass and rate of production on a ground area basis are synthesised from growth data and the interaction between plant density and growth is considered. Differences in dry weight partitioning show that the highest proportions of below ground tissue and standing dead matter are found at the more severe sites. Investment of dry weight into reproductive structures increases with site favourability although this is more true of auxilliary reproductive structures than of actual propagules.

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In the dwarf shrubs, dry weight changes in perennating tissue are followed throughout the life cycle and are compared between sites. Dry weight changes are also described at a more detailed level for individual young shoots, deciduous and non-deciduous habits being contrasted. Both perennating tissue and young shoots show increases in dry weight with site favourability, generally mirroring the trend found in Polygonum viviparum, but bud dry weight is shown to be least at the more favourable sites. Age class structures of the dwarf shrub populations are compared and the fast turnover of Salix lapponum from the Norwegian wet meadow contrasted with the great longevity of Vaccinium vitis-idaea from Finland. From these data, long term inferences on population stability are made.

From data on dry weight changes and plant densities, total biomass and rates of production are synthesised and compared between sites, the interaction between the two processes being described.

INTRODUCTION

The biomass of a population or community is fundamentally determined by an interaction between the abundance of individuals (resulting from the dynamics of the population) and the dry weight of these individuals (growth) (Callaghan, 1973).

Whereas the dry weight of an individual is, to a certain degree, a reflection of environmental stresses, it is largely determined by a genetically controlled range of plasticity (there are minimum and maximum dry weights possible for a given species beyond which survival is impossible) and by the stage of the life cycle, or age, attained by the individual. Where a range of life cycles is available, the particular life cycle followed by an individual (often selected by the environment) will impose its own limits on growth at any particular stage.

The density of individuals on a ground area basis is determined by the numbers present at a given time in the past, and the proportion of these which die together, with the numbers of new offspring produced between the two times. However, the mortality and natality rates depend directly upon the ages, or stages in the life cycle, attained by the individuals present at that given time in the past. In a predominantly vegetatively reproducing graminoid, for example, old individuals may show high mortality rates and low rates of production of new offspring: this leads to decreasing plant density with time. In a given population, however, individuals of all possible ages would be expected and this is commonly found, although populations, like individual plants, follow life cycles. In colonising stages, large numbers of young and no old individuals are present, whilst the converse applies in degenerating populations. Thus the age class structure of a population is important in determining plant densities.

By synthesising biomass changes per unit ground area from data on growth throughout the life cycle and population dynamics, the significance of processes underlying biomass can be assessed. In addition, many critical points in the life cycle are available for detailed studies of environmental and genetic control of individual processes.

This method of biomass estimation allows detailed comparisons between the biomass in two or more areas. Similar biomass at two sites, for example, may be determined by different dry weight/density relationships, the superficial similarity being interpreted through differences in growth and population structure.

This paper compares plant growth forms at several of the international tundra sites. The methods are extensions of those used in the Bipolar Botanical Project (Lewis and Callaghan, 1970; Callaghan and Lewis, 1971; Callaghan, 1973). Two growth forms (herbaceous perennial and dwarf shrubs)

are compared at all possible levels of growth throughout the life cycle, and comparisons of population maintenance are made. Differences and similarities in these processes are illustrated between the two growth forms and biomass, together with rates of production, is synthesised from these more basic data wherever possible. A major source of error in the determination of biomass from area sampling techniques arises from differences in floristic composition or plant densities between samples. The comparisons of the growth of individual plants and their components in the present paper are independent of this source of error. However, comparisons of overall biomass changes will also be made in a future paper by another tundra biome working group.

MATERIALS, SITES AND METHODS

Material

Species were selected from each of the four main growth forms, i.e. forbs, dwarf shrubs, graminoids and bryophytes, from as many sites as possible, the first two groups being dealt with here.

Of the forbs, a ubiquitous species (Polygonum viviparum) was chosen. This species was sampled from five national sites and from two extreme habitats within each site, wherever possible (a favourable sheltered, floristically rich meadow on one hand and a severe exposed floristically poor fell-field on the other; Lewis and Callaghan, in press). Within the dwarf shrubs, however, different species were sampled from two habitats. The dwarf shrubs were chosen as species showing ecological similarities and occupying analagous niches at all the various sites.

Although the taxonomic variation between the dwarf shrub species is far greater than between different populations of Polygonum viviparum from different sites, ecological similarities enable valid between-site comparisons to be made. Even within Polygonum viviparum, considerable genetic differences

can exist resulting, to some extent, from different ploidy levels (Engell, 1973). The genetic differentiation between populations from different sites may be thought of as a response to particular environments. To some extent, the species differences between the dwarf shrubs at the various sites may be considered to be a response to environmental differences. This, together with niche similarities, allows valid between-site comparisons of dwarf shrubs. In addition, between-site comparisons of one growth form include a smaller source of error resulting from genetic differences than between-site comparisons of overall biomass for communities often represented by different growth forms.

Sites

During 1972 visits were made to the following I.B.P. tundra sites: Niwot Ridge, Colorado; Barrow, Alaska; Devon Island, Canada; Stigstuv, Norway; Kevo, Finland, and Glenamoy, Ireland. Sites not visited during the present project, but where previous comparitive data had been collected are located on South Georgia in the sub-Antarctic, and Disko Island, West Greenland. In addition, comparative data to be included at the final synthesis are also available from Signy Island, Antarctica; Abisko, Sweden, and Moor House, England.

Collections of species considered in the present report were made at the sites described in Table I. Floristic and environmental site descriptions have not been included as they are available elsewhere.

Methods

Each species was harvested, pressed and dried at the various sites. Concurrent with harvesting, estimates were made of the densities of plants and/or aerial shoots of some dwarf shrubs. Material was also kindly collected

TABLE I

A site list for the collections of *Polygonum viviparum* and dwarf shrubs, including the species of dwarf shrubs sampled.

Sites	*Polygonum viviparum*	Dwarf shrubs
Niwot Ridge, Colorado		
Edge of *Kobresia* meadow	✓	-
Between *Kobresia* meadow and snow bed site	-	*Salix planifolia*
Kevo, Finland		
Sub-alpine heath	-	*Vaccinium vitis-idaea*
Disko Island, Greenland		
Primary site (luxuriant herbslope)	✓	*Salix glauca*
Fell-field site	✓	*S. glauca*
Stigstuv, Norway		
Wet meadow	✓	*S. lapponum*
Dry meadow	✓	*S. reticulata*
Barrow, Alaska		
Beach ridge (gas-line ridge)	✓	-
Meadow (behind field huts at Site 2)	✓	-
Exposed and raised polygon centre (between meadow and creek)	-	*S. pulchra*
Devon Island, Canada		
Beach ridge (transition zone)	✓	-
Intensive meadow (northern borders)	✓	*S. arctica*

by workers at the various sites for other relevant times during the growing season. About 25 dwarf shrub plants were harvested from most of the sites, but only 10 of the extremely large plants could be harvested from Kevo and Niwot Ridge. Sample sizes of young shoots, however, always exceeded 30. In Polygonum viviparum, 16 flowering and 16 vegetative plants were collected from each habitat at each harvesting date.

The plant collections were analysed into the various components described in the following sections and plant tissues were oven dried at 80° C for 48 hours.

Statistical analyses consisted of single classification analysis of variance for plant dry weights at a given time and step-wise curvi-linear regressions (Callaghan, 1973) on plant weights over the life cycle. Least significant differences are not included with the single classification analysis of variance because of the differences in magnitude between all the various comparisons. Standard errors presented graphically are the maximum standard errors for a given parameter, and when presented with regression lines, they represent the maximum standard error for any point on the regression line.

LIFE CYCLES

The majority of tundra plant species are perennials, with annuals almost completely unrepresented (Bliss, 1971) and they typically show efficient means of vegetative propagation (Sørensen, 1941; Billings and Mooney, 1968). Sexual reproduction may be completely lacking as in Polygonum viviparum (Engell, 1973) or lacking in some species under particular environmental conditions as in Phleum alpinum during short growing seasons (Callaghan, 1973). Even where sexual reproduction occurs efficient vegetative propagation of tundra species often results in extensive clones. Where underground organs

(graminoids and some forbs) or prostrate aerial shoots (dwarf shrubs) are instrumental in this type of proliferation, complex and extensive interconnected "systems" exist. The physiological independence of any part of these "systems" is at present poorly understood, but some data have been obtained on the grass Dupontia fischeri (Allessio and Tieszen, 1973), Phleum alpinum (Callaghan, 1973) and mosses (Collins and Oechel, 1974) whilst other data are presented in this report.

Occasionally, clones exist of a species represented by numerous but completely independent units. These units must be physiologically independent and they are perhaps best exemplified by Polygonum viviparum.

Life cycle of Polygonum viviparum

Reproduction takes place vegetatively by bulbils produced on spikes below any flowers, where these are present. The number of culms per plant varies according to the genotype (Engell, 1973) and site (Table II). Sexual reproduction may be completely lacking and flower production varies (Engell, 1973; see Table II). Bulbils germinate on reaching moist ground at any time during the growing season and require approximately ten days for this process on moist filter paper in the laboratory. Roots and leaves are produced and a rhizome develops between the point of insertion of the petioles and the bulbil; the bulbil may remain attached to the rhizome for many years.

Out of approximately six hundred plants investigated, none showed vegetative reproduction resulting from division of the rhizome. Thus, each plant remains an individual and the plant dies as a whole unit although death of above ground organs occurs each autumn (See Fig. 1) and the rhizome senesces from its point of attachment to the bulbil whilst growing from the meristematic region at soil level.

The annual production of leaves is increased by production of leaf bearing culms and inflorescences in older plants. More than one culm per plant may be produced in any one year (see above) and during some years no

TABLE II

A between-site comparison of reproductive parameters for plants of *Polygonum viviparum*

Site	Harvest date	% of culms flowering	No. of culms per plant	No. of bulbils per culm	No. of bulbils per plant	Mean weight per bulbil (in mg)	% of final development
Niwot Ridge	15/7	36.59	1.375	36.5	50.18	1.009	100
Norway Dry Meadow	30/7	86.36	1.375	29.22	40.18	.826	100
Norway Wet Meadow	2/8	91.67	1.125	20.68	23.27	1.272	100
Devon Intensive Meadow	17/8	20.00	1.125	20.21	22.74	.291	63
Devon Beach Ridge	11/8	0.00	1.000	18.19	18.19	.383	97
Barrow Beach Ridge	4/8	45.71	1.063	18.76	19.94	.514	98
Barrow Meadow	4/8	3.64	1.125	10.22	11.5	.353	100
Significance of F. Value			*	***	***	***	

culm may be formed. The current year's above ground tissue is surrounded by a sheathing non-photosynthetic bract. Part of this bract is persistent for many years after death and removal reveals a scar on the rhizome. Occasionally, it has been possible to count these scars and age plants from a wet habitat, where rhizomes are elongated vertically. Table III shows the relationship between age and total live dry weight on the Devon Island Intensive Meadow. No replication was possible.

Polygonum viviparum differs from most tundra species in that it shows a very simple life cycle, individuals remaining as discrete plants due to lack of vegetative reproduction in underground organs. A vegetative plant therefore, can either die or produce a culm and inflorescence - it cannot produce another plant as in the case of dwarf shrubs, graminoids, some mosses and many herbaceous perennials.

Life cycles of dwarf shrubs

An important feature of the dwarf shrub growth form is the high proportion of non-assimilating perennating tissue and the restriction of assimilating tissue to specialised shoots. Fig. 2 compares the proportion of perennating tissue to seasonal growth in a graminoid, herbaceous perennial and dwarf shrub. Associated with this increase in perennating tissue in dwarf shrubs is an increase in longevity, and the vast resources stored in this tissue become increasingly important as growing seasons decrease in length, particularly in snow bed habitats.

New assimilating tissue is inevitably produced from an over-wintering bud. Buds are developed in the axils of leaves of current years shoots and their dry weight remains constant over the first, dormant year in Salix reticulata (see Fig. 3d). Following winter, and the breaking of dormancy, the bud axis elongates and leaves are produced. During this season, a woody

TABLE III

The relationship between dry weight and age in Polygonum viviparum from the Devon Island intensive meadow site.

Age (years)	Total live weight (in g)
0 (bulbil)	.0003
1	.0055
11	.0796
12	.1217
16	.1031
26	.0821

stem, leaves and their axillary buds, and occasionally catkins are produced (see Fig. 3); this whole unit is termed a current year's shoot throughout this report. During autumn leaf fall occurs in deciduous species such as Salix reticulata, leaving only stem and axillary buds to over-winter. These two components form the unit shown as last year's shoot in Fig. 3d. In subsequent years, this shoot increases in dry weight as annual rings are formed. The width of the annual ring formed provides a comparative measure of annual growth (see Table IV). Thus the seasonal growth of dwarf shrubs may be divided into the production of assimilatory and reproductive structures from buds and the addition of an annual ring of xylem and other tissues in the perennating portion of the plant.

In some deciduous species the axillary buds may be differentiated at an early stage, vegetative buds producing a current year's shoot with leaves, and reproductive buds (usually terminal) developing either into a current year's shoot bearing a few leaves and catkins (S. reticulata and S. arctica) or an inflorescence which is itself equivalent to the current year's shoot (Myrica gale and S. pulchra). Current year's shoots bearing catkins may be extremely modified, having only a few leaves (S. arctica) or they may not differ from vegetative current year's shoots (S. reticulata). Where terminal reproductive structures exist, growth is sympodial, resulting from the death of the apical meristem following flowering. In M. gale this results in considerable wastage of dry weight because of the relatively great spatial separation of terminal buds forming inflorescences and the lateral bud forming vegetative current year's shoots. After death of the inflorescence, the intervening length of last year's shoot then dies.

In tundra regions, the evergreen habit is of great importance (Bliss, 1971) in economising on the dry weight of assimilatory tissue and in providing extra storage tissue in the older leaves. The longevity of

TABLE IV

Mean width of annual rings in tundra dwarf shrubs modified from Warren Wilson (1964) to include comparative data from I.B.P. tundra sites. For all other references see Warren Wilson (1964).

Locality	Ring width (mm)	Reference
Devon Island (76°N)	.14	author
Cornwallis Island (75°N)	.07	Warren Wilson (1964)
East Greenland (74°N)	.21	Kraus (1874)
Barrow, Alaska (71°N)	.11	author
North Finland (70°N)	.71	Hustich (1948)
North Finland, Kevo sub-alpine heath (70°N)	.10	author
North Siberia (69°N)	.54	Middendorff (1867)
Russian Lappland (68°N)	.41	Kihlman (1890)
Baffin Land (67°N)	.16	Ambronn (1890)
South Finland (65°N)	1.11	Hustich (1948)
South Greenland (63°N)	.69	Warming (1888)
Norway, Hardangervidda (60°N)		
Salix reticulata	.13	author
Salix lapponum	.08	author
South Alaska (59°N)	2.73	Cooper (1931)
Ireland, Glenamoy (54°N)	.53	author
United States, Niwot Ridge, Colorado (40°N)	.40	author

assimilatory tissues varies from the deciduous habit described above, to the mainly short-lived leaves of Vaccinium vitis-idaea (see Fig. 4) and the long-lived leaves of Cassiope tetragona (see Fig. 5).

Reproduction usually takes place both vegetatively and sexually. Sexual reproduction is demonstrated by the presence of many inter-specific hybrids in the Salix genus at the Norwegian sites, for example, although vegetative production is far more frequent. In erect shrubs, e.g. Salix glauca from the Disko Island Primary site, layering occurs when aerial shoots are pressed onto a moist soil/moss surface by the weight of overlying snow. On the other hand, prostrate shrubs e.g. Vaccinium vitis-idaea from Kevo, produce roots along their creeping aerial branches. In both erect and prostrate shrubs, new plants are produced when an old branch dies and a younger rooted branch becomes separated from the parent plant gaining its own physiological independence. This method of propagation results in off-spring attaining considerable ages before they can be classed as individuals. The lack of young individuals in the age class distribution histograms (see Figs. 6 and 7) is explained both by this and the comparative rarity of sexual reproduction.

PATTERNS OF GROWTH AND DEVELOPMENT

Patterns of growth and development in Polygonum viviparum

Because plant age was often difficult to determine, seasonal changes in weight are presented for random flowering plants and these are described from three sites.

At the beginning of season, nearly all the living dry weight is found in the rhizome and there is an equal dry weight of standing dead matter (Fig. 1). Roots are also present at this time, with, at Niwot Ridge (Fig. 1), a small dry weight component of leaves. As the season progresses, the rhizome increases in weight, root weight remains fairly constant and the leaves increase in dry weight at Niwot Ridge, or new leaves are produced, as at the two Barrow sites.

At all three sites, reproductive structures increase in dry weight. Some reproductive tissue is represented at the Barrow meadow site at the beginning of season, in the form of bulbils, which were formed during the previous growing season and remained attached to dead culms through the winter. These bulbils are still viable but as the present season progresses they are lost as old culms decay and new reproductive structures are formed.

Plants growing at Niwot Ridge (Fig. 1) show maximum dry weights earliest in the growing season whilst the Barrow meadow plants show an earlier maximum than those of the Barrow beach ridge, which only obtain maximum dry weights at the end of season. In the longer growing season of Niwot Ridge, the early production of maximum dry weights allows more time for death and decrease in dry weight of above ground tissues so that only rhizome, root and standing dead matter is found at the end of season, although the rhizome itself also shows considerable loss of weight. At the Barrow sites, although leaf dry weight decreases towards the end of season, the dry weight of reproductive structures increases slightly and the rhizome shows a much higher dry weight than it does at the beginning of season. The time at which the rhizome must subsequently decrease in dry weight before the start of the following season is not known.

The maximum dry weights of the various components differ not only in the time of growing season at which they are achieved, but also in their magnitude (Table V). Total living and total living plus standing dead show a trend from very high values at the Niwot Ridge and Disko Island sites to low values at the Barrow and Devon Island sites. The difference between the maximum (Niwot Ridge) and minimum (Barrow meadow) dry weights of total living matter are eighteen fold.

Considerable differences exist between the extreme habitats within a given locality, although the two habitats sampled in Norway are not as different as the extremes in other localities. Surprisingly the most severe site at Hardangervidda, the lichen heath, did not support Polygonum viviparum. However, the more severe habitats within a locality at the higher end of the range of dry weights

(the Greenland fell-field and Norwegian wet meadow site) show higher dry weights than the more favourable habitats in a more severe locality. Thus, the Greenland fell-field site shows lower dry weights than the Greenland primary site but higher dry weights than the Norwegian dry meadow site. Similarly, the Norwegian wet meadow site shows lower dry weights than the dry meadow but higher dry weights than the Devon Island intensive meadow. At the lower end of the scale of dry weights this distinction does not hold, the Barrow meadow showing higher dry weights than the Devon Island beach ridge.

The distribution of living dry weight between the various plant tissues shows that the highest proportion is consistently allocated to the mainly perennating below ground tissue (Table V). Reproductive structures also possess a high dry weight investment with photosynthetic tissue somewhat lower. Whilst the dry weight of below ground and reproductive tissue shows the trend described for total dry weight, the dry weight of leaves shows a more confused pattern in that plants from the Norwegian dry meadow and the Barrow beach ridge show lower dry weights than those found at their more severe counterparts, i.e. the Norwegian wet meadow and the Barrow meadow respectively. The Greenland fell-field shows an unexpectedly low leaf and reproductive dry weight. Standing dead matter shows unusually high dry weight at the Devon Island intensive meadow and Norwegian dry meadow site.

The dry weight of below ground tissue (rhizome plus root) relative to total dry weight shows that the greatest investments into perennating tissue are shown by the severe Devon Island, Barrow and Greenland fell-field sites (Table VI). These sites also show proportionally more standing dead relative to living matter, but the Nivot Ridge site shows an equally high proportion of standing dead. Where higher investment into reproductive tissues might be expected at the severe sites, as is seen in the dwarf shrubs for example (see below), in fact the opposite is found. Thus proportionally more dry weight is allocated to reproductive structures at the Niwot Ridge, Greenland primary and Norwegian sites (Table VI). However, this reproductive tissue is mainly structural

TABLE V

A between-site comparison of the maximum dry weight (g) of Polygonum viviparum plants and their components

Site	Harvest date	Below ground	Leaves	Reproductive	Total living matter	Total dead matter	Total live + dead matter
Niwot Ridge	15/7	.3903	.1181	.1294	.6378	.2622	.9000
Greenland Primary	15/8	.3032	.1093	.1566	.5691	.0672	.6363
Greenland Fell-field	15/8	.2766	.0142	.0217	.3125	.0594	.3719
Norway Dry Meadow	30/7	.1707	.0272	.0843	.2822	.0865	.3687
Norway Wet Meadow	2/8	.1087	.0364	.0830	.2281	.0434	.2715
Devon Island Intensive Meadow	17/8	.0935	.0197	.0110	.1242	.0553	.1795
Devon Island Beach Ridge	11/8	.0671	.0093	.0099	.0863	.0442	.1303
Barrow Beach Ridge	21/8	.0745	.0066	.0241	.1052	.0458	.1510
Barrow Meadow	4/8	.0357	.0087	.0056	.0500	.0150	.0650
Significance of F value †		***	***	***	***	***	***

† The Greenland sites are not included in the statistical analyses.

TABLE VI

A between-site comparison of dry weight partitioning in *Polygonum viviparum*

Site	Harvest date	Reproductive/total living	Dead/total living	Below ground living/above ground living
Niwot Ridge	15/7	0.213	0.464	1.723
Greenland Primary	15/8	0.275	0.118	1.140
Greenland Fell-field	15/8	0.069	0.190	7.705
Norway Dry Meadow	30/7	0.305	0.292	1.600
Norway Wet Meadow	2/8	0.360	0.200	0.946
Devon Island Intensive Meadow	17/8	0.092	0.434	3.218
Devon Island Beach Ridge	11/8	0.119	0.536	3.730
Barrow Beach Ridge	21/8	0.233	0.471	2.836
Barrow Meadow	4/8	0.107	0.305	2.659
Significance of F value †		***	***	***

† The Greenland sites are not included in the statistical analyses.

rather than directly in propagules. A very low reproductive investment is shown by the Greenland fell-field site.

During the production of a culm, dry weight per unit length increases. This can be seen at the Barrow beach ridge site where development continues until the end of season (Table VII and Fig. 1). After death of the culm there is a loss in dry weight over several years until the dead culms are physically detached. The loss in dry weight per unit length of culm provides a measure of weight losses due to translocation and/or decay. At the Devon beach ridge, for example, the weight/length ratio is 1.3010 ± 0.059 in the year of production of the culm when the culm is living and this falls to 0.9863 ± 0.072 after one year and 0.6282 ± 0.039 after two years. The rate of loss in the first year, immediately following death is usually much faster than that of the second year (Table VII). A very high rate of dry weight loss is shown by culms from the Norwegian wet meadow during the year of their production (Table VII). High rates of loss are also shown by plants from Niwot Ridge during both years and by plants from the Devon Island intensive meadow during the second year. Low rates of loss are shown by plants from both Barrow sites.

Thus, Polygonum viviparum shows a decrease in total plant weight with site severity, and an increase in the proportion of dry weight allocated to standing dead, below ground and reproductive tissues. After the death of reproductive structures, low rates of translocation and/or decay are shown by the severe Barrow sites. The species also shows a delay in the attainment of maximum individual plant biomass with site severity or reduction in the length of the growing season.

Patterns of growth and development in dwarf shrubs

a. Perennating tissue

Accumulation of perennating tissue is most rapid at the high alpine site of Niwot Ridge where the maximum plant age was only 30 years (Fig. 8).

T A B L E VII

A between-site comparison of translocation/decay rates in Polygonum viviparum as measured by changes in culm weight per unit length (mg/cm). Standard errors are given.

SITE	YEAR OF PRODUCTION				YEAR AFTER PRODUCTION			
	Culm weight per unit length (mg/cm)				Culm weight per unit length (mg/cm)			
	Early Season	Late Season	Time interval (days)	Rate of loss (mg/cm/day)	Early Season	Late Season	Time interval (days)	Rate of loss (mg/cm/day)
Niwot Ridge	3.722±0.327	2.629±0.331	55	.0198	2.369±0.168	1.551	95	.0086
Norway wet meadow	2.860±0.214	1.790±0.097	32	.0334	—	—	—	—
Devon Island Intensive meadow	—	—	—	—	1.105±0.044	0.974±0.211	13	.0101
Barrow beach ridge	1.322±0.046	1.476±0.047	17	.0090*	1.032±0.047	0.922±0.088	66	.0016
Barrow meadow	0.894±0.074	0.641±0.042	17	.0148	0.762±0.053	0.626±0.055	66	.0023

* rate of gain during living phase rather than a rate of loss (see Fig. 1b)

Similar dry weights were produced by Vaccinium vitis-idaea growing at the sub-alpine heath, Kevo. In this species however, the high dry weights were produced over a much longer time interval, the oldest plant sampled being 109 years old. High dry weights were also obtained for the Disko Island primary and fell-field sites (see Fig. 9) but the weights presented are under-estimates since they only apply to above ground tissues. However, as in the case of Polygonum viviparum, although great differences occur between the favourable primary site dry weights and the lower ones at the severe fell-field site, the fell-field site still shows values higher than the remaining national sites when the below ground dry weight is also considered. The low dry weights at the fell-field site are associated with greater longevity. At the remaining sites, Salix pulchra at Barrow show a higher rate of accumulation of living tissue but proportionately less standing dead than S. arctica from the Devon Island intensive meadow (Fig. 8). Both species of Salix at Hardangervidda in Norway show very low rates of accumulation of living and standing dead matter and they also show shorter life spans than all but the above ground shoots of Salix glauca at the Disko Island primary site. Although data were obtained for only the above ground shoots of Myrica gale at Glenamoy, these show a rapid increase in both living and standing dead dry weight over a six year period (Fig. 9). No aerial shoots over six years old were found, and considerable numbers of completely dead aerial shoots occurred.

Associated with these rates of accumulation of dry matter are the width of the annual rings. Thus high ring widths are found at Niwot Ridge and Glenamoy whilst low values are found at the high arctic and Norwegian sites (Table IV). A comparison with data quoted by Warren Wilson (1964) shows generally lower values at the I.B.P. sites than for other sites at comparable latitudes (Table IV), but certain data quoted however, may represent maximum measurements, and not average ring widths for a particular region.

b. Young shoots

As described above, young shoots are produced from over-wintering axillary buds. These accumulate weight slowly during their year of production (see Fig. 3) but after the breaking of dormancy, stem, leaves and reproductive tissues are formed which quickly reach a maximum dry weight at the Barrow site. The stem, with its axillary buds, is retained at the end of season to become next year, last year's shoot, whilst leaves and reproductive structures are lost in all of the Salix species.

On Devon Island, dry weight increases quickly after dormancy has broken but the maximum is achieved far later in the growing season than at Barrow. This situation may be compared with the immaturity of Polygonum viviparum plants on Devon Island at a comparatively late point in the growing season. In Norway Salix lapponum only achieves maximum dry weight of current year's shoots at the end of the growing season and reproductive tissue is completely lacking (Fig. 3c). This may result from the possible hybrid nature of the plant at the wet meadow site. S. reticulata however, achieves maximum dry weight earlier in the season and produces fully matured catkins (Fig. 3d). In both Norwegian species, the last year's shoots decrease slightly in dry weight over the growing season.

A completely different pattern of growth of young shoots is shown by the evergreen Vaccinium vitis-idaea from Finland (Fig. 4). After the breaking of dormancy, the extremely small buds (see Table VIII) produce a woody stem and a much greater dry weight investment occurs in leaves than in the species of Salix. Flowers are produced in the first year but their dry weight is extremely small compared with that of assimilating tissue. During the second and third years, the stem continues to increase in dry weight but the assimilating tissue decreases in dry weight due to abscission of leaves, the dry weight of attached dead leaves remaining very small. The rate of increase in the stem dry weight is reduced during the remaining years whilst the rate

of decrease in assimilatory tissue increases until all the leaves are lost. Thus, the maximum life span of a leaf in this species is five years whilst the majority of leaves survive for three years or less.

In Cassiope tetragona from the rock out-crop site on Devon Island, leaf length varies with the point during the growing season at which the leaf was produced (see Fig. 5). This may also be found in many graminoids and mosses. As leaves can be aged as a result of differences in leaf length, it can be seen that senescence of leaves takes place after six years in the case of Cassiope tetragona (Fig. 5). After the onset of senescence, leaves remain attached to the stems for a considerable period of time. Flower buds and vegetative buds (i.e. those producing lateral branches) are formed in the axils of living leaves. The increase in size of a given leaf from year to year is probably a result of the life cycle pattern of a given shoot in that as a young shoot matures, the leaves it produces may increase in size (years 12 to 7 in Fig. 5) but as the shoot senesces, its leaves may not achieve the lengths of earlier formed leaves (years 7 to 1 in Fig. 5). Thus, a particular shoot may only be able to produce a given number of leaves before it dies.

A comparison of the maximum dry weights achieved by the current year's shoots of the various dwarf shrubs (Table VIII) shows that the highest dry weights are attained at the more favourable Glenamoy and Kevo sites whilst very low values are shown at the Norwegian and Devon sites. Salix pulchra at Barrow shows an unexpectedly high dry weight of total living matter. The dry weights of stem plus buds and leaves show a similar trend to the dry weight of total living matter. Reproductive tissue however, shows very high dry weights at the severe Barrow and Devon Island sites, but at Kevo, the investment into reproductive structures is very small, with no reproductive tissue found at all in Salix lapponum at the Norwegian wet meadow site. Dead leaves were only found attached to current year's shoots at Kevo and Glenamoy but this may be the result of late season sampling at these two sites. Bud dry weight at the beginning of season (see Table VIII) tends to show a

TABLE VIII

A between-site comparison of dry weight partitioning in current year's shoots of tundra dwarf shrubs at the stage of their maximum development

Site	Species	Early season Minimum dry weight (g)	Maximum dry weight (g)					
		Bud	Stem + buds	Leaves	Reproductive	Total living	Total dead	Harvest date
Niwot Ridge	Salix planifolia	.0017	-	-	-	-	-	-
Glenamoy	Myrica gale	.0008	.0969	.0705	.0039	.1713	.0045	3/10
Kevo, sub-alpine heath	Vaccinium vitis-idaea	.0004	.0080	.0625	.0008	.0713	.0007	21/8
Norway Wet Meadow	Salix lapponum	.0008	.019	.025	0.0	.044	0.0	3/9
Norway dry Meadow	S. reticulata	.0019	.0069	.0161	.0034	.0264	0.0	6/8
Barrow	S. pulchra	.0031	.0162	.0450	.0191	.0803	0.0	15/7
Devon Island Intensive Meadow	S. arctica	.0013	.0082	.0278	.0077	.0437	0.0	17/8
Significance of F. values		***	***	***	*	***		

negative correlation with site severity in that comparatively large buds are found at the Barrow, Devon Island and Norwegian dry meadow sites whilst very small buds are found at Kevo and Glenamoy.

POPULATION DYNAMICS

Population dynamics of Polygonum viviparum

The maintenance and establishment of populations of Polygonum viviparum is effected mainly by the production and dispersal of vegetative bulbils; sexual reproduction has not yet been demonstrated (Engell, 1973). Flowers are produced at some sites however, and between eighty-six and ninety-two percent of all culms possessed flowers at the Norwegian sites whereas few culms possess flowers at the two Devon Island and Barrow meadow sites (Table II). This may be a reflection of stresses on development due to short growing seasons. Flowers are produced at the apex of the inflorescence after the bulbils have been formed, maximum development being achieved at sites where flowering is common (Table 2). In order to assess the stage of development of culms at a site, the mean length of this year's culms has been divided by the mean length of entire last year's culms. Thus, whereas the two Norwegian and Niwot Ridge sites with the longest growing seasons show maximum development, the Devon Island sites show immature reproductive structures. The high percentage of culms flowering at the Barrow beach ridge site is somewhat anomalous.

The size and stability of populations will ultimately depend upon the number of propagules produced and their viability, their numbers depending upon the numbers of flowering plants present (Table IX), the number of bulbils per culm and the number of culms per plant (Table II): viability can be inferred from the mean dry weight per bulbil.

The number of culms per plant shows little variation between sites with a maximum of 1.375 at the Niwot Ridge and Norwegian dry meadow sites (Table II). However, these values are all generally low, up to nine culms per plant having been reported by Engell (1973) for other areas. The number of bulbils per

culm shows the same trend as the number of culms per plant at all but the Barrow meadow site. This leads to greater between-site variation in the number of bulbils per plant. The high number of culms per plant and bulbils per culm lead to very high values of bulbils per plant at the favourable Niwot Ridge and Norwegian dry meadow sites. Lower values are shown by the Arctic sites and particularly by the Barrow meadow site.

High density of flowering plants at the Norwegian dry meadow and Devon beach ridge sites (Table IX) leads to high production of bulbils on a ground area basis (1924 and 432 bulbils $/m^2$ respectively) whereas the low densities of flowering plants at the Barrow meadow and beach ridge sites leads to very low production of propagules on a ground area basis (24 and 80 bulbils/m^2 respectively. Although the Devon beach ridge site differs from the intensive meadow site by showing lower values for the number of culms per plant and the number of bulbils per culm (Table II), the higher density of flowering plants at the beach ridge site (Table IX) leads to a higher production of propagules on a ground area basis (432 compared with 276 bulbils/m^2). Thus, although the reproductive capacity per plant may be associated with site favourability, the reproductive capacity per ground area depends upon other factors, the most important perhaps being seedling survival as influenced by the physical environment and competition.

Seedling survival can to some extent, be facilitated by the production of large propagules with high energy stores. As the energy stores increase, the period during which the seedling can develop before becoming self-sufficient increases. This will lead to a delay in the effects of competition, by which time the seedling is better able to compete. Bulbil weight again shows a trend associated with site favourability, the Niwot Ridge and Norwegian sites showing the highest dry weights (Table II). However, the 3.5 fold difference between maximum and minimum dry weight (the Norway wet meadow and Barrow meadow sites, neglecting the diseased bulbils of the Devon Island intensive meadow) is less than the 4.5 x difference between the total living dry weight

at these sites. This difference is even more marked when the 3 x difference in the mean bulbil dry weight between the Niwot Ridge and Barrow meadow site is compared with the 13 x difference in total living dry weight. Thus, although bulbil weight decreases with site severity, the rate of decrease is far less than for total dry weight, resulting in an increase in dry weight investment in bulbils as site severity increases. This gives the propagules at the more severe sites a proportionally better chance of survival than at the favourable sites.

Population dynamics of dwarf shrubs

Consideration of the population dynamics of dwarf shrubs is restricted to an examination of plant density, distribution of age classes, and within the plant itself, the number of current year's shoots.

The number of current year's shoots per plant increases with age in all species (Fig. 10), and the rate of increase closely follows the pattern described for the rate of increase in total live wood per plant (Fig. 8). Thus, Salix arctica and S. reticulata show low rates of increase in live wood with age and also low rates of increase in the number of current year's shoots with age. On the other hand, S. planifolia and Vaccinium vitis-idaea show rates of increase in the number of current year's shoots with age approximately 10 times greater than the remaining dwarf shrubs (Fig. 10).

At Glenamoy, the number of current year's shoots per above ground branch increase very rapidly with age during the short life span of the above ground branches (Fig. 11). This situation is also found at the two Greenland sites. It can also be seen from Fig. 11 that there is considerable mortality of current year's shoots at Glenamoy. This mortality takes place at a comparatively late stage of development of the current year's shoot, unlike the situation at the remaining sites, where mortality more often occurs by the failure of buds to break dormancy.

Plant density varies considerably between sites (Table X). Low densities are found at the rocky sub-alpine heath in Finland, whereas a very high density of Salix lapponum is found at the Norway wet meadow site. However, the sparse Vaccinium vitis-idaea plants at Kevo possess considerably more dry weight than the abundant Salix lapponum plants at the dry meadow in Norway. The remaining species all grow at similar densities.

It can be seen (Fig. 6e) that the numerous plants of S. lapponum at the Norwegian wet meadow show a rapid turn-over; no plants survived the 21-25 year age class, whilst 46% of all plants belong to the 6-10 year age class. An even faster rate of turn-over is shown by above ground branches of Myrica gale (see Fig. 7c) but these branches may be expected to show higher turn-over rates than whole plants.

S. planifolia from Niwot Ridge (Fig. 6a) also shows a high rate of turn-over with 50% of the plants between 26 and 30 years old, whilst S. reticulata shows an earlier mode but slightly greater longevity. Plants from Barrow and Devon Island tend to show greater longevity and a more even distribution of age classes, whilst the greatest longevity, the most even distribution of age classes and the oldest mode is shown by Vaccinium vitis-idaea at the sub-alpine heath, Kevo.

On Disko Island (Fig. 7) the greatest longevity is shown by the fell-field population which also shows a mode at a greater age than the primary site population.

Young plants are conspicuously lacking from all except the Norwegian and Glenamoy sites which perhaps arises as a result of the method of vegetative propagation described earlier.

TOTAL BIOMASS AND RATES OF PRODUCTION

Total biomass and rates of production in Polygonum viviparum

The biomass of Polygonum viviparum at any time depends upon the interaction between the number of plants per ground area and their dry weights. Plants have been divided into vegetative and flowering, vegetative plants being younger and

possessing less dry weight (Table IX). At the beginning of season, however, the two cannot be distinguished and the dry weight of the plant in early season may lead to an under estimate of the rate of production of vegetative plants and an over estimate of the rate of production of flowering plants. These will tend to cancel one another giving a more accurate estimate of overall production rates.

Vegetative plants show greater densities than flowering plants at each site, the greatest density being shown by plants at the Devon Island intensive meadow site. High densities are also shown by the Norwegian sites and the Devon Island beach ridge site whilst the two barrow sites show low densities.

Although dry weight per plant differs between the two Barrow sites by only 1.5 x, the 2.5 x difference in plant density interacts to produce very different biomass estimates at the beginning of season (Table IX). Maximum plant weight differs more than minimum plant weight between the two sites and this leads to even greater biomass differences, which are reflected in the higher rates of production, despite the longer growing season, at the Barrow beach ridge site. However, both rates of production are very low when compared with those for dwarf shrubs, as is discussed below.

The data available for maximum biomass at other sites show that the greatest biomass is achieved at the Devon Island intensive meadow site. This is, to some extent, the result of higher vegetative plant dry weights but is also determined by the higher plant densities. In view of the low flowering plant dry weights, the higher vegetative plant weights are somewhat anomalous but may be the result of the vegetative plant category containing many plants where floral initiation has taken place but floral development has not progressed sufficiently for the plant to be recognised as flowering. It will be remembered that all flowering plants were, in any case, immature at this site (Table II).

Both Norwegian sites show considerably higher biomass than the Barrow sites, and the Norwegian dry meadow shows greater biomass than the wet meadow as the result of higher plant density and the greater dry weights of flowering plants

TABLE IX

A between-site comparison of maximum and minimum biomass and rates of production of Polygonum viviparum

Site	Number of vegetative plants/m^2 ± one standard error	Number of flowering plants/m^2 ± one standard error	MINIMUM Mean plant dry weight (g)	MINIMUM Biomass (g/m^2)	MAXIMUM Mean vegetative plant dry weight (g)	MAXIMUM Mean flowering plant dry weight (g)	MAXIMUM Biomass (g/m^2)	Time interval between maximum and minimum biomass (days)	Rate of production (g/m^2/day)
Norway Wet Meadow:									
living tissue	70.40 ± 12.53	14.88 ± 4.46	—	—	.0803	.2282	9.0487		
living + dead tissue					.1064	.2716	11.5320	—	—
Norway Dry Meadow:									
living tissue	85.60 ± 27.87	18.08 ± 5.89	—	—	.0745	.2822	11.4794		
living + dead tissue					.0977	.3687	15.0242	—	—
Devon Island Intensive Meadow:									
living tissue	110.72 ± 17.10	11.52 ± 3.76	—	—	.0935	.1242	11.7831		
living + dead tissue					.1430	.1795	17.9008	—	—
Devon Island Beach Ridge:									
living tissue	62.72 ± 12.90	23.68 ± 7.04	—	—	.0612	.0861	5.8761		
living + dead tissue					.0846	.1303	8.3946	—	—
Barrow Beach Ridge:									
living tissue	20.67 ± 5.09	3.65 ± 0.90*	.0367	.8925	.0841	.1052	2.1223	66	.0186
living + dead tissue			.0705	1.7146	.1123	.1517	2.8749		
Barrow Meadow:									
living tissue	8.98 ± 4.40	1.79 ± 0.77*	.0272	.2872	.0283	.0500	.3331	49	.0062
living + dead tissue			.0499	.5269	.0353	.0650	.4197		

* only the total number of plants per metre square were obtained at the Barrow sites and these have been partitioned into flowering and vegetative plants using the average ratio from the other sites.

TABLE X

A between-site comparison of biomass and rates of production in tundra dwarf shrubs

Site	Species	Number of plants/m^2 ± one standard error	Number of current year's shoots/m^2	Minimum living biomass (g/m^2)	Maximum living biomass (g/m^2)	Interval between maximum and minimum biomass (days)	Rate of productio (g/m^2/day
Kevo, sub-alpine heath	Vaccinium vitis-idaea	3.67	278.00	107.378	131.885	89	0.275
Norway Wet Meadow	Salix lapponum	38.00 ± 8.60	1344.34	143.829	201.904	85	0.683
Norway Dry Meadow	S. reticulata	11.23 ± 2.30	282.60	44.730	51.981	57	0.127
Barrow	S. pulchra	12.80 ± 3.40	1115.73	212.138	298.272	40	2.153
Devon Island Intensive Meadow	S. arctica	8.96 ± 5.92	286.88	53.365	65.762	40	0.310
Disko Island Primary Site	S. glauca*	——	——	1550.0	3590.0	81	25.185
Glenamoy	Myrica gale*	8.11 ± 1.97	2577.87	161.187	439.750**	ca.200	1.393

* data apply to above ground biomass only

** dead current year's shoots are included in this estimate

at the dry meadow site (see Table IX).

The high levels of propagule dispersion shown by this species together with considerable longevity suggest that yearly biomass fluctuations will be comparatively small, particularly as plant density is one of the most important biomass determinants. Thus, during a given growing season, the environment will determine mean plant dry weight to some extent and the number of propagules produced. Plant density, however, will be relatively unaffected in all but the most extreme conditions. This comparatively stable situation is similar to that found in the longer-lived dwarf shrubs (see below) and contrasts strongly with the population explosions and subsequent die-back of Phleum alpinum (Callaghan, 1973). As in the case of dwarf shrubs (see below) plant density estimates give the greatest variance in determining biomass.

Total biomass and rates of production in dwarf shrubs

The biomass of a dwarf shrub per unit area of ground at a given time depends upon many of the processes previously described. It will ultimately depend upon the number of current year's shoots per metre square, the mean weight of a current year's shoot and the weight of perennating tissue per metre square.

The number of current year's shoots per metre square is calculated by summing the products of the number of current year's shoots (Fig. 10) for each age class of bush present (Fig. 6) and the number of plants per metre square of that age class (Table X). From the number of current year's shoots per metre square and the mean dry weight of these shoots at any given time (Figs. 3 and 4), the total biomass of current year's shoots per metre square can be found and this can be added to the previously calculated dry weight of perennating tissue per metre square to yield the total biomass on a ground area basis. The calculations are summarised as follows:

$$\text{BIOMASS at any given time} = \sum (WtP_i \times M_i)_{1-N} + \left(\sum (C_i \times M_i)_{1-N} \times WtS \right)$$

where WtP_i = dry weight of perennating tissue for age i at that time

M_i = number of bushes of age i per metre square

N = number of plants of different ages present

C_i = number of current year's shoots per bush for age i

WtS = mean dry weight of a current year's shoot at the given time

The relationship between seasonal production and annual production of perennating tissue on an individual plant basis can be seen in Figs. 12 and 13. High proportions of seasonal growth are seen in Salix pulchra and S. lapponum. In Vaccinium vitis-idaea, a high proportion of seasonal production relative to perennating tissue is found throughout most of the life cycle. On an above ground basis only, very high seasonal production relative to above ground perennating tissue can be seen at both Greenland sites and at Glenamoy. This is the result of both high numbers of current year's shoots per bush (Fig. 11) and high mean dry weights per current year's shoot (Table VIII).

At a more detailed level, Fig. 14 shows the increase in perennating tissue and the seasonal fluctuations in the tissues of current year's shoots over three years during the life span of Salix reticulata from the Norwegian dry meadow. At the beginning of season, buds break dormancy and the total compartment decreases in weight as more buds form current year's shoots, these being made up of leaves, stems and catkins as described elsewhere. At the end of season, leaves and reproductive structures are lost, new axillary buds over-winter to form the next year's current year's shoots, and the stem becomes part of the next year's perennating tissue. In addition, dry weight is added to older perennating tissue giving the slight within season increase in perennating tissue shown in Fig. 14.

When the dry weights of perennating tissue and seasonal growth is expressed on a ground area basis, very high above ground biomass is found at

the Greenland primary site (Table X) due to high values shown by all the contributory factors, including the number of current year's shoots per above ground branch, the dry weight of perennating tissue per above ground branch, branch density and young shoot dry weight (M.C. Lewis and B.J. Phillips pers. comm.). Although Vaccinium vitis-idaea also shows high values for most of these parameters, the relative sparsity of plants at the site leads to low biomass values (Table X). On the other hand, the high plant densities of Salix pulchra and S. lapponum have lead to relatively high biomass estimates for these slow growing plants. Low plant densities and slow growth leads to the low biomass estimates of S. arctica and S. reticulata.

Differences between maximum and minimum biomass divided by the time interval between these phases yield rates of production (see Table X). By far the highest rate of production is found on Disko Island, whilst the short growing periods on Devon Island and at Barrow lead to the high rates of production in S. arctica and S. pulchra. On the other hand, the high rate of production of Salix lapponum during a comparatively long growing season is due mainly to a high rate of increase in the number of current year's shoots per plant with age, and the high dry weights of these shoots. Low rates of production are shown by Vaccinium vitis-idaea due to a long growing season and low plant density and by Salix reticulata as a result of low values in all contributory parameters.

The high rate of production of above ground tissues in Myrica gale, despite its exceptionally long growing season, is due almost entirely to the production of current year's shoots, each with very high dry weight investments.

By synthesising biomass and rates of production in the above manner, it can be seen that growth rates may show little relationship to overall productivity. This is exemplified by the high growth rates of Vaccinium vitis-idaea together with its low rate of production on a ground area basis. This method of biomass synthesis also allows an assessment of the levels of importance of the various contributory factors. For example, the productivity of Myrica gale is

fundamentally determined by the numbers and weight of current year's shoots interacting with the long growing season.

Limited data on population dynamics may also lead to long term inferences. Species with a rapid turn-over of plants, e.g. Salix lapponum, may be expected to show the most rapid changes in biomass due to succession and community change. On the other hand, long-lived species like Vaccinium vitis-idaea, will take many years to show differences in its contribution to overall community biomass because at least some of the twenty year old plants now present would be expected to survive for another ninety years and the great increase in dry weight of plants with age would compensate for the loss of younger plants.

Over a shorter time interval, it has been seen that seasonal production is mainly contributed by the interaction of the number of current year's shoots and the mean dry weight of these. In any correlations with environmental conditions the environment within a given growing season will determine the mean dry weight of a current year's shoot. However, it is the environment of the previous growing season which determines the number of buds formed in that season and hence the number of current year's shoots in the present season. The biomass in any given season, therefore, is dependent upon the environment of at least two seasons, and as the number of current year's shoots may be a more important variable than their mean dry weight, the environment of the previous season may be far more important than that of the present season in determining biomass.

The method of estimating biomass described above also allows an assessment of inaccuracies involved. Where plant density is low and the sparse plants are large, for example, predictions of biomass over a large ground area become difficult because of the great variation in the estimates of plant densities due to complex spatial distributions of individual plants. Thus, in the case of Salix arctica from Devon Island, although changes in dry weight of current year's shoots, and even whole plants, can be monitored quite accurately the very

large variation in spatial plant density (Table V) leads to inaccurate estimates of biomass per unit ground area. When plant density is high, e.g. S. lapponum and Myrica gale, changes in plant distribution become less significant and the variance of biomass estimates per unit ground area is reduced. It is important however, that plant performance can be compared from the detailed level of current year's shoots to the more general level of biomass and production rates per unit ground area.

ACKNOWLEDGEMENTS

I would like to thank The Royal Society of London for the visiting research fellowship which enabled this work to be carried out. My thanks are also due to the heads of the Department of Botany, University of Manchester, and the Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancashire, for the many facilities made available to me.

I am extremely grateful to Dr. O.W. Heal of Merlewood Research Station for valuable help and advice throughout the initiation of the project and its subsequent administration. D. French of the same research station helped considerably with the plant analyses and this is gratefully acknowledged. I would also like to thank Dr. M.C. Lewis of the Department of Botany, University College, Dublin for help and advice during the initiation of the project and both Dr. Lewis and Miss B.J. Phillips for making available unpublished data on Salix glauca from Greenland.

This project would have proved impossible without the considerable help and support received from the national site co-ordinators and their staff at all the sites visited. In particular, I would like to thank, in order of sites visited, Dr. P.J. Webber and Mrs. D. May, Niwot Ridge; Dr. L.L. Tieszen, Dr. P.C. Miller, Miss S. Vetter and Mr. K. Sutherland, Barrow; Professor L.C. Bliss, Dr. G. Courtin, Mr. M. Muc and Mr. J. Svoboda, Devon Island; Professor F.E. Wielgolaski and Mr. S. Kjelvik, Norway; Dr. L. Kärenlampi, Finland; Dr. M. Sønesson and

Dr. J. Flower-Ellis , Sweden; Professor J.J. Moore and Mr. G. Doyle, Ireland.

Finally, I would like to thank Mrs. E. Callaghan for technical assistance throughout the project and Miss C.H. Jackson and Mr. N.J. Collins for help with preparation of the manuscript.

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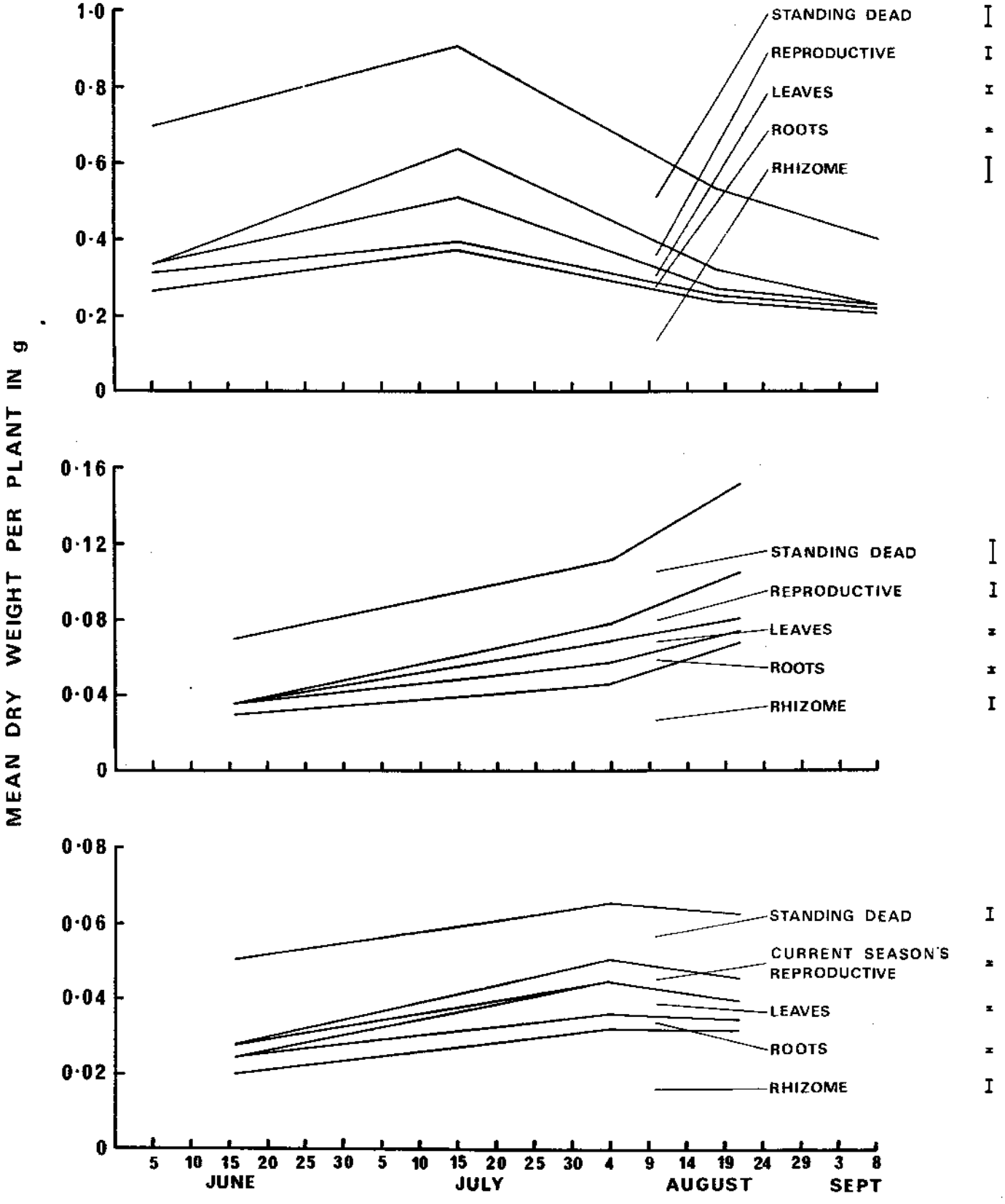
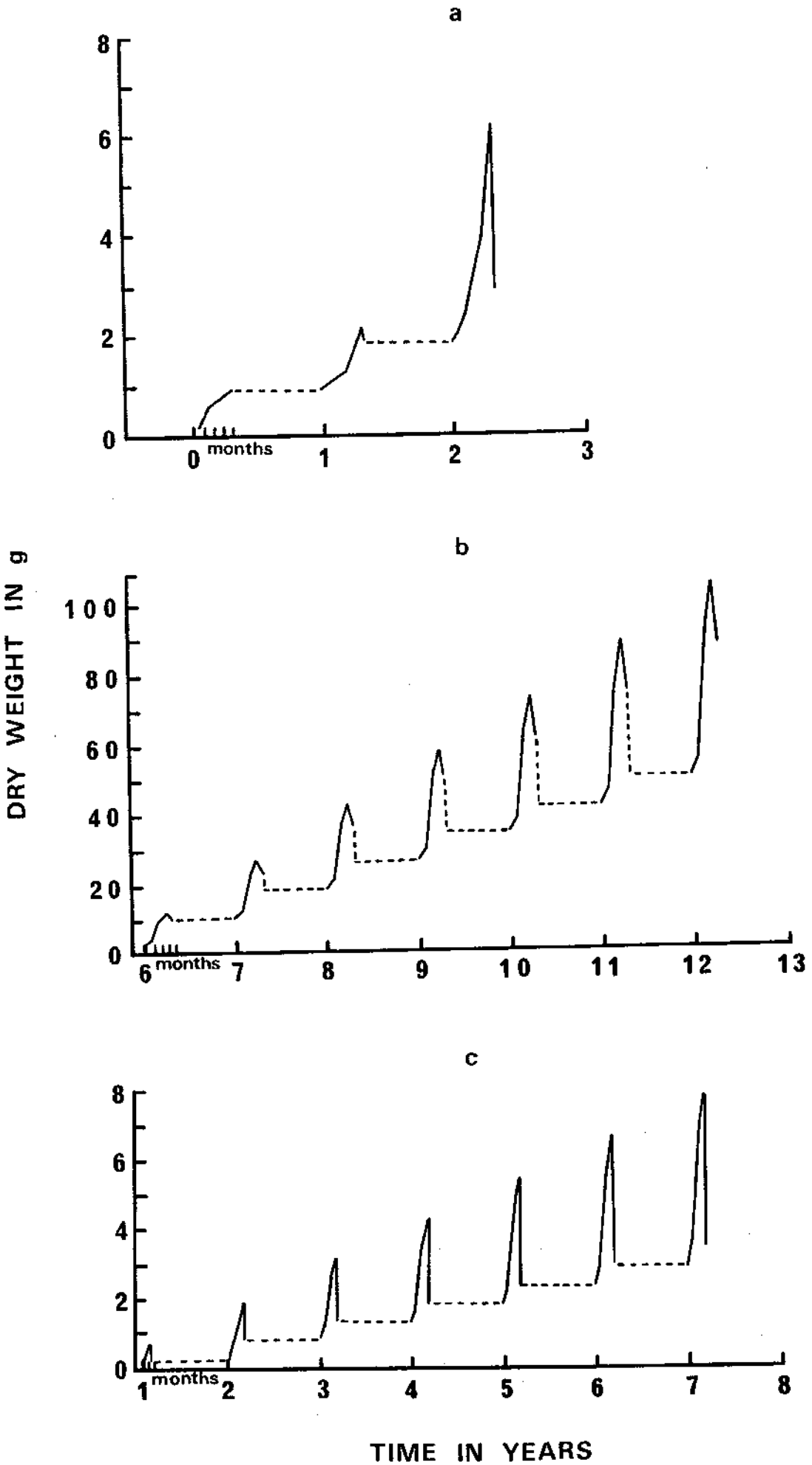
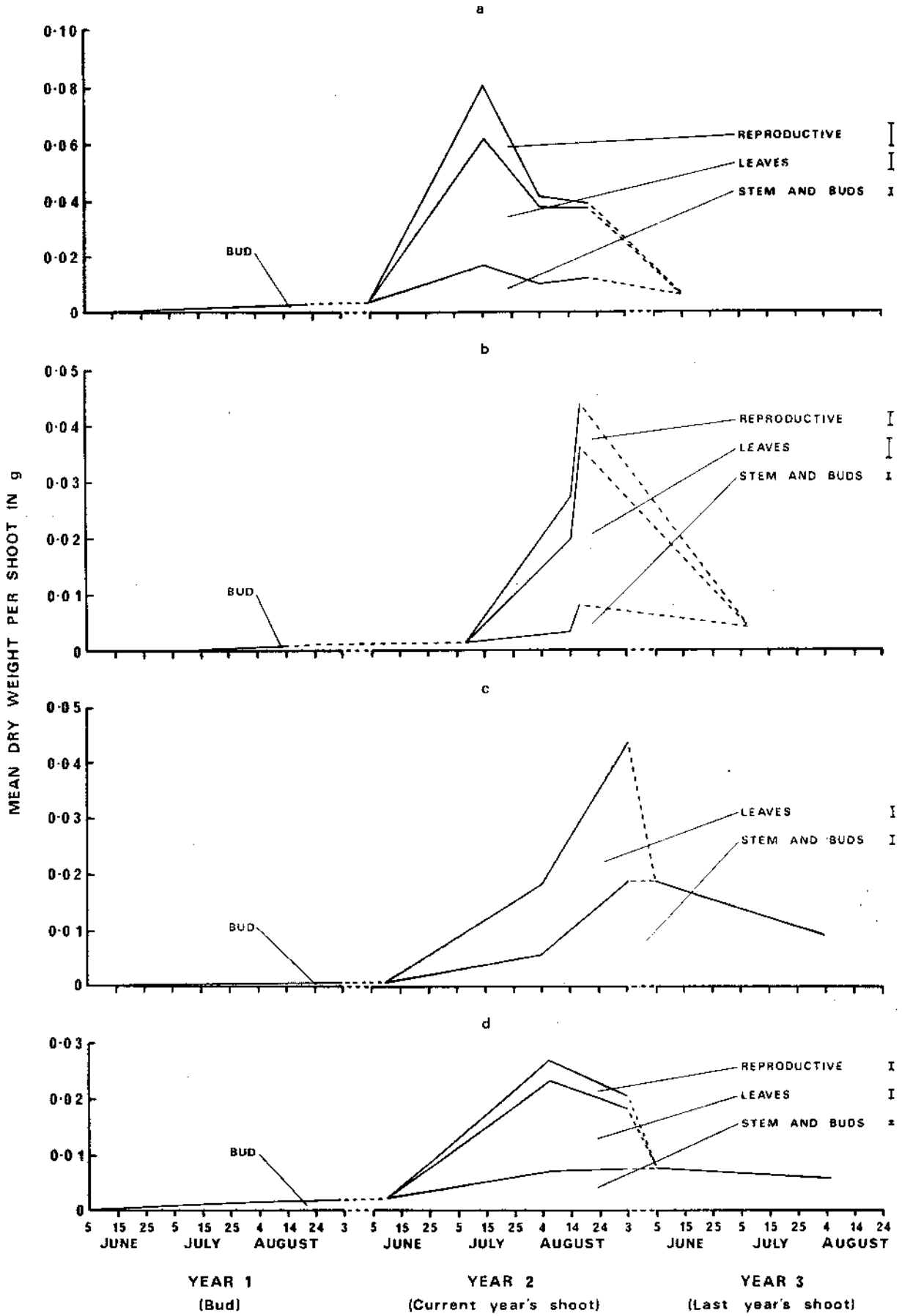


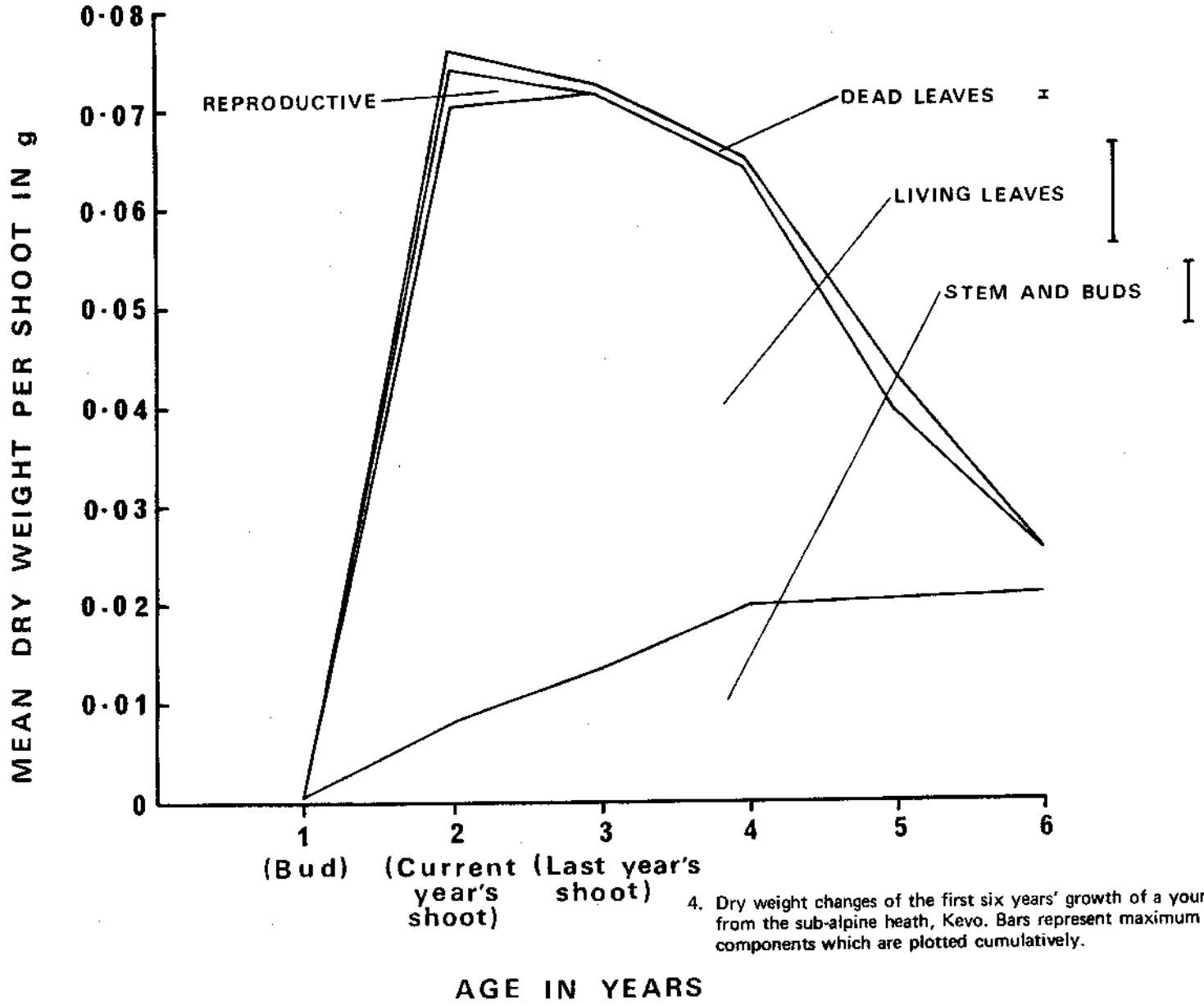
1. A between-site comparison of the changes in dry weight of plant structures, plotted cumulatively, in *Polygonum viviparum*. a. Niwot Ridge; b. Barrow, beach ridge; c. Barrow, meadow. Bars represent the maximum standard errors for each plant compartment.
N.B. The data are presented on different scales.



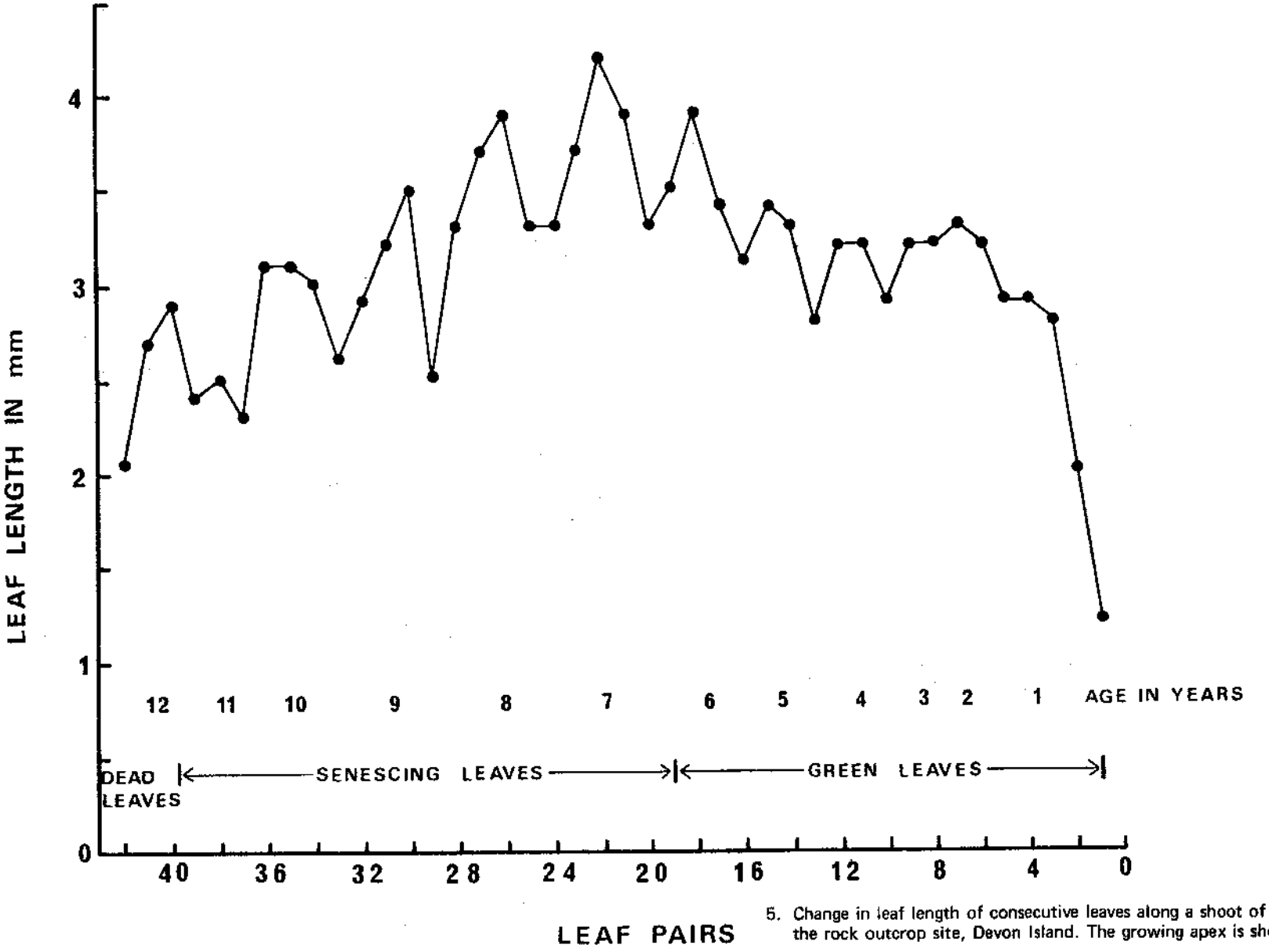
2. Distorted sine-wave simulation of the growth in dry weight of individual plants of a. *Phleum alpinum*; b. *Salix glauca* and c. *Alchemilla glomerulans*. A sine-wave is fitted to minimum and maximum seasonal biomass for random age classes and distorted so that the peak coincides with the period of maximum biomass. The amplitude represents seasonal growth of ephemeral tissue whilst the wave-length represents the length of the growing season.



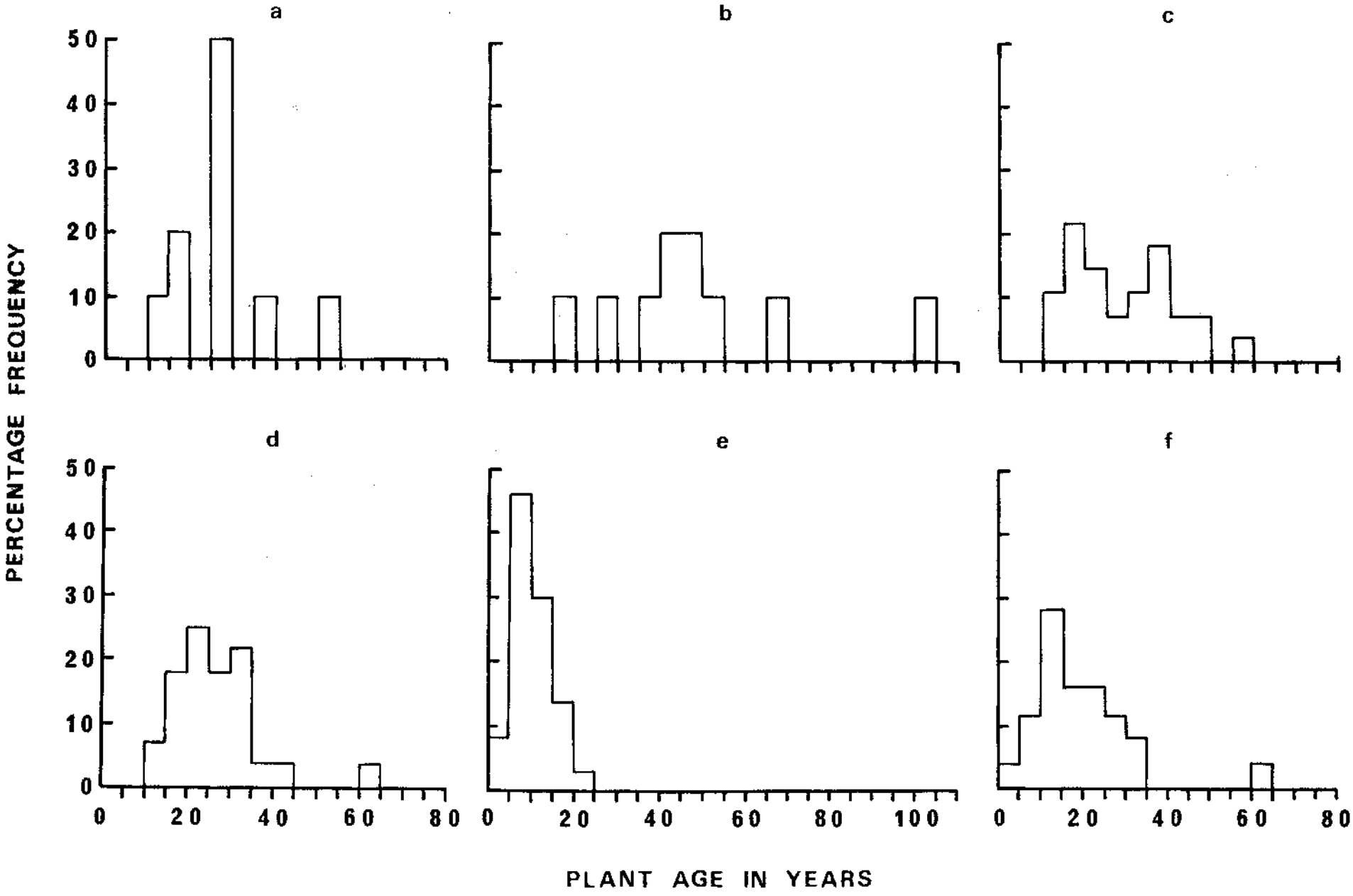
3. A between-site comparison of the growth of young shoots in tundra dwarf shrubs. a. *Salix pulchra,* Barrow; b. *S. arctica,* Devon Island intensive meadow; c. *S. lapponum,* Norway wet meadow, d. *S. reticulata,* Norway dry meadow. Bars represent the maximum standard errors of the various plant components which are plotted cumulatively.
N.B. The data for a. is plotted on a different vertical scale than for the other species.



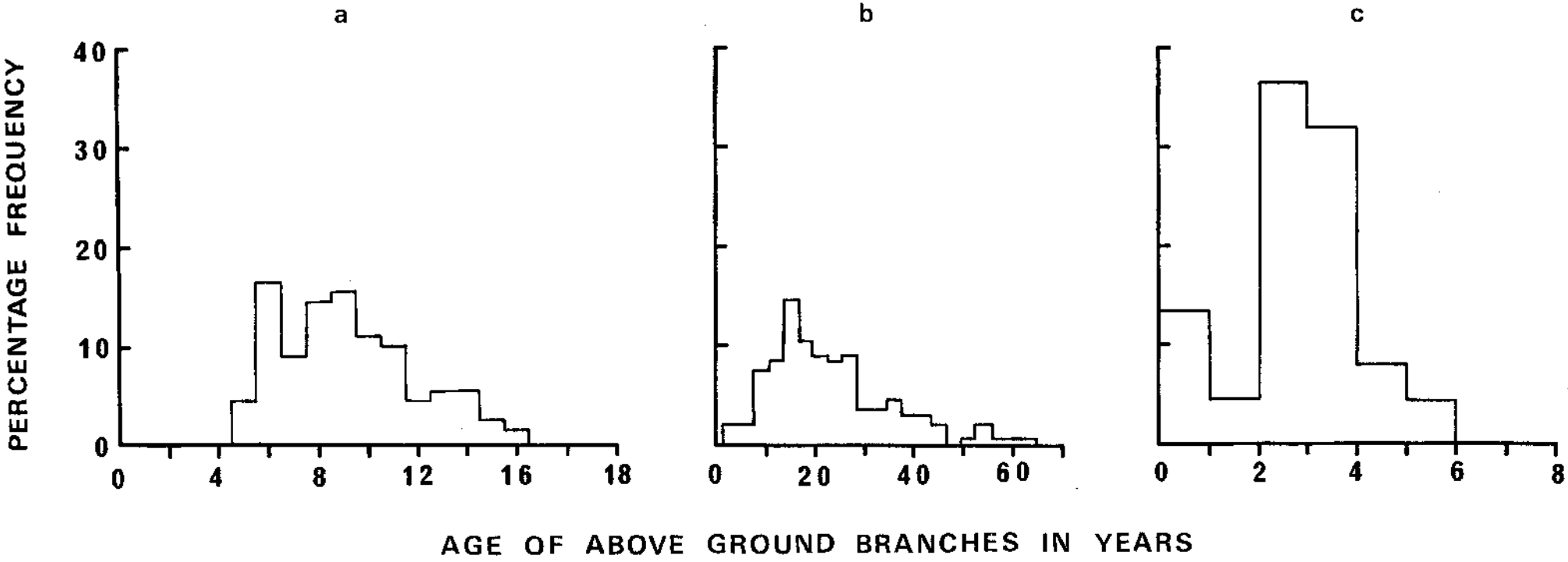
4. Dry weight changes of the first six years' growth of a young shoot of *Vaccinium vitis-idaea* from the sub-alpine heath, Kevo. Bars represent maximum standard errors for the various plant components which are plotted cumulatively.



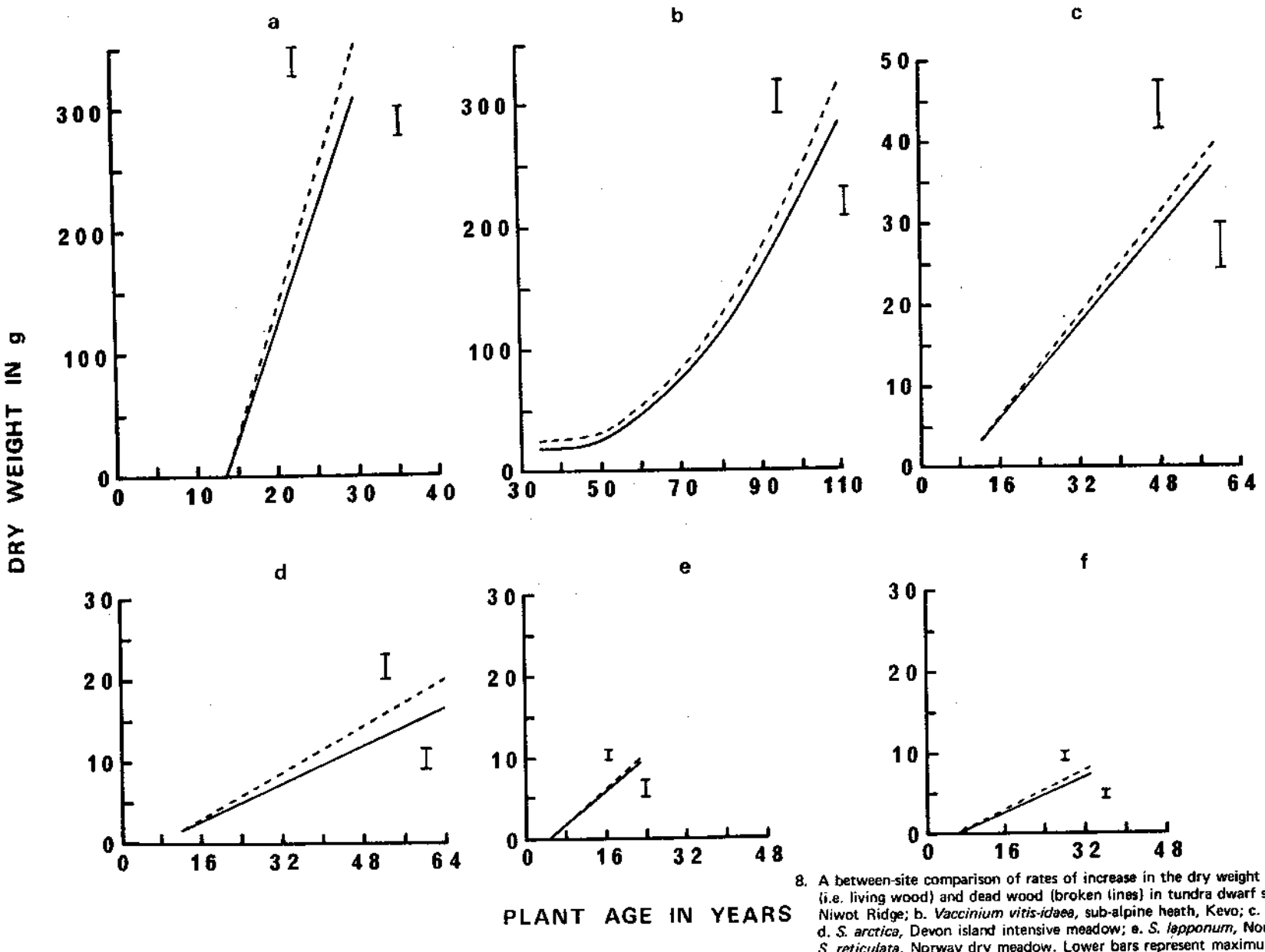
5. Change in leaf length of consecutive leaves along a shoot of *Cassiope tetragona* from the rock outcrop site, Devon Island. The growing apex is shown to the right hand side.



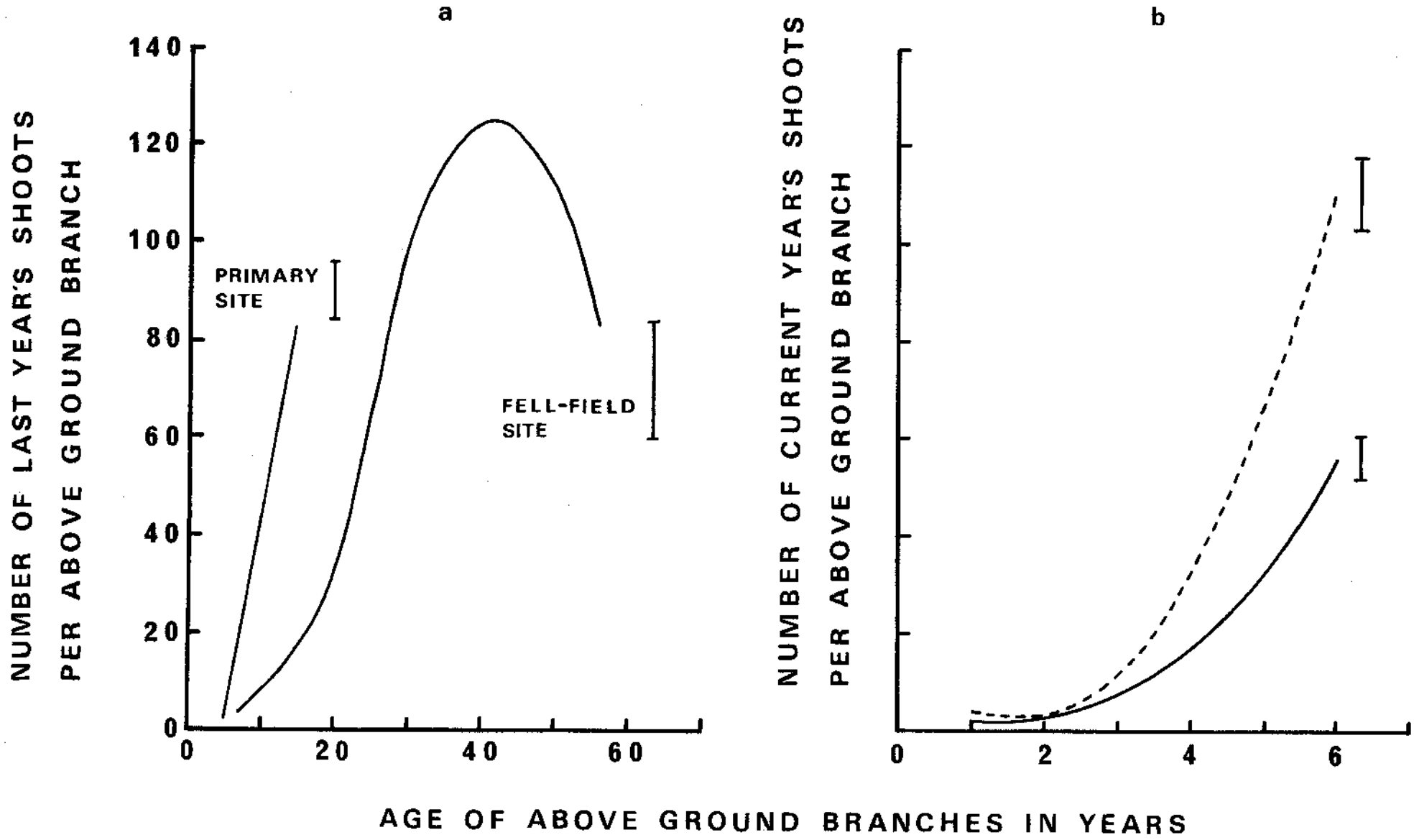
6. A between-site comparison of age class distribution in tundra dwarf shrub plants. a. *Salix planifolia,* Niwot Ridge; b. *Vaccinium vitis-idaea,* sub-alpine heath, Kevo; c. *Salix pulchra,* Barrow; d. *S. arctica,* Devon Island intensive meadow; e. *S. lapponum,* Norway wet meadow; f. *S. reticulata,* Norway dry meadow.



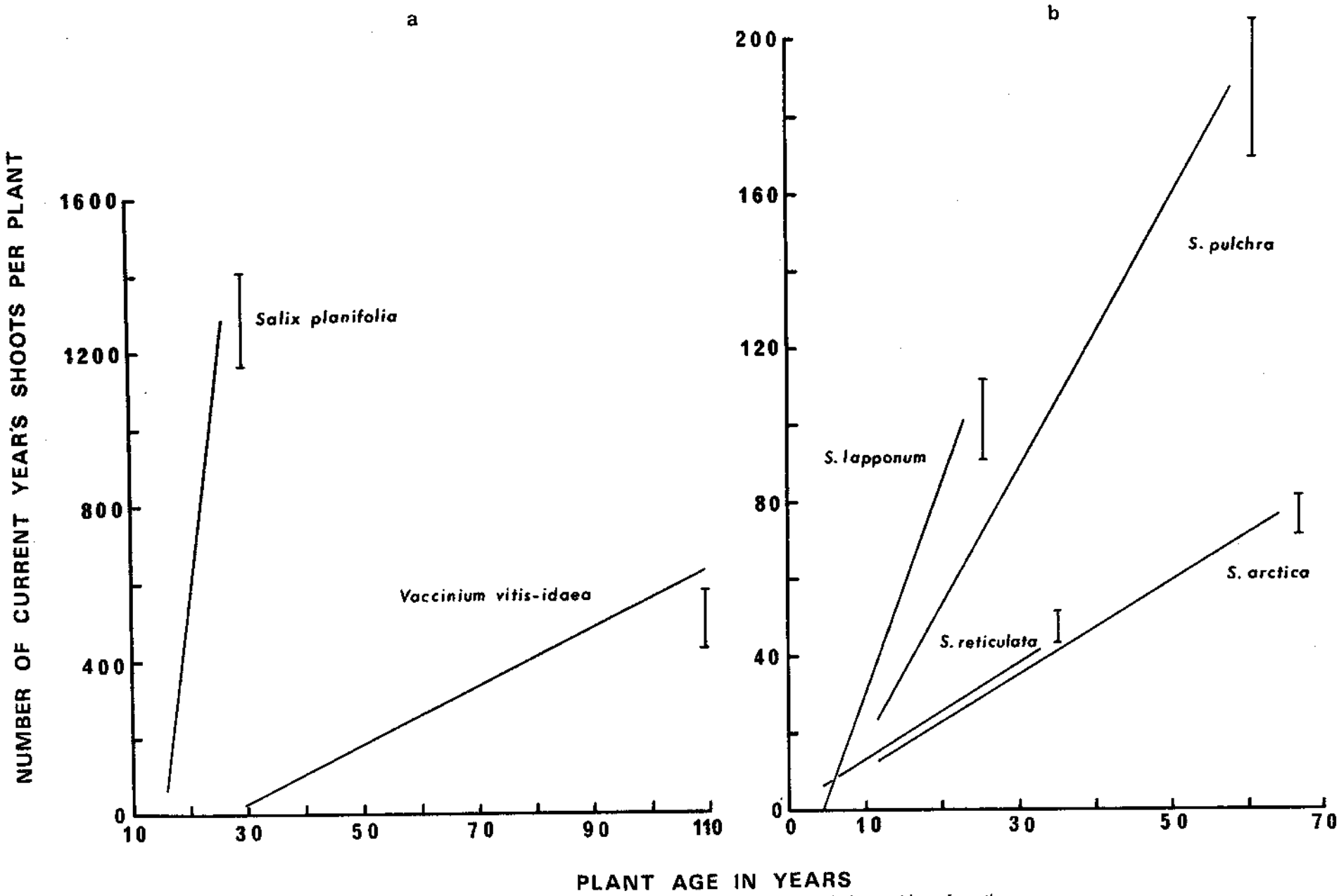
7. A between-site comparison of age class distribution in the above-ground branches of tundra dwarf shrubs. a. *Salix glauca,* Disko Island primary site; b. *S. glauca,* Disko Island fell field and c. *Myrica gale,* Glenamoy.
N.B. The data are presented on different scales.



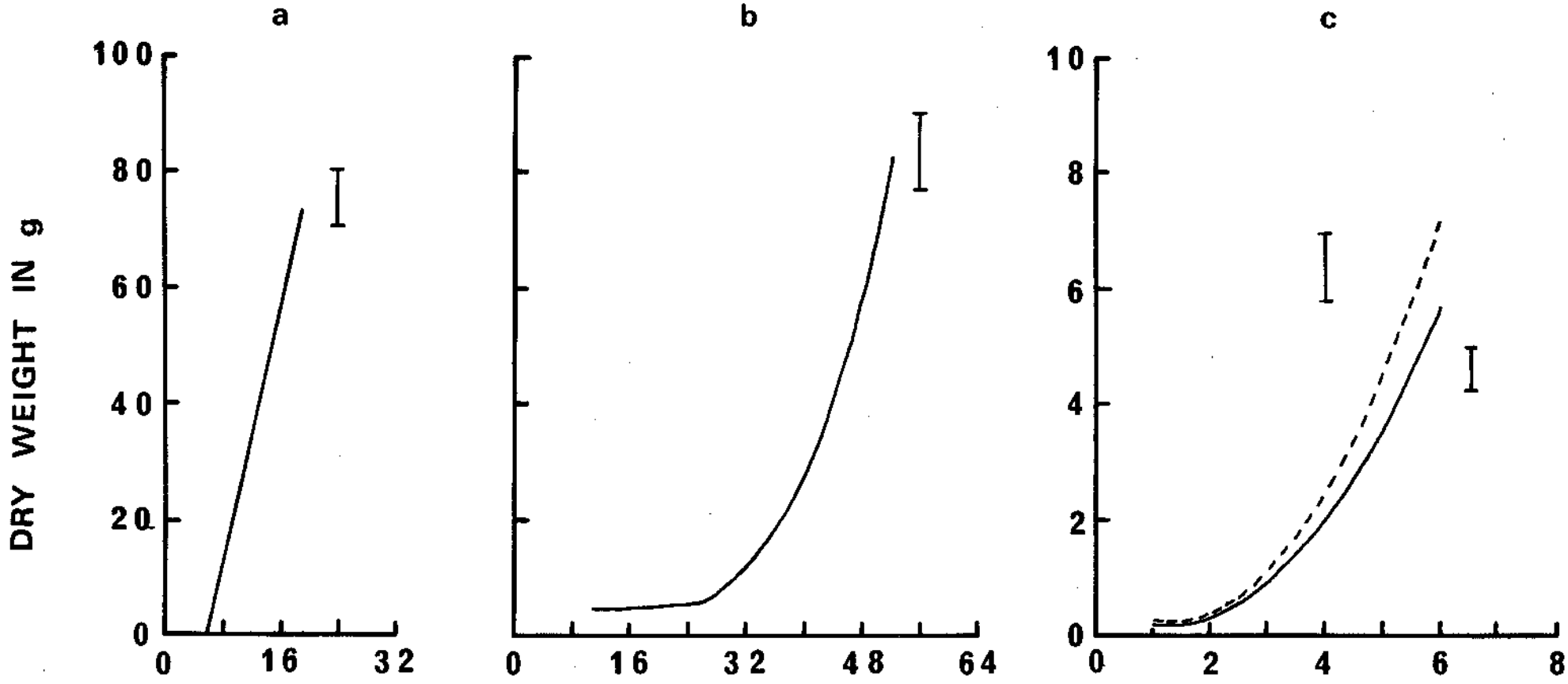
8. A between-site comparison of rates of increase in the dry weight of total perennating tissue (i.e. living wood) and dead wood (broken lines) in tundra dwarf shrubs. a. *Salix planifolia*, Niwot Ridge; b. *Vaccinium vitis-idaea*, sub-alpine heath, Kevo; c. *Salix pulchra*, Barrow; d. *S. arctica*, Devon island intensive meadow; e. *S. lapponum*, Norway wet meadow and f. *S. reticulata*, Norway dry meadow. Lower bars represent maximum standard errors of total living, whilst upper bars represent maximum standard errors of total living plus standing dead matter. All regression lines are at least significant at the .05 level.
N.B. Data for a. and b. are presented on different scales from remaining data.



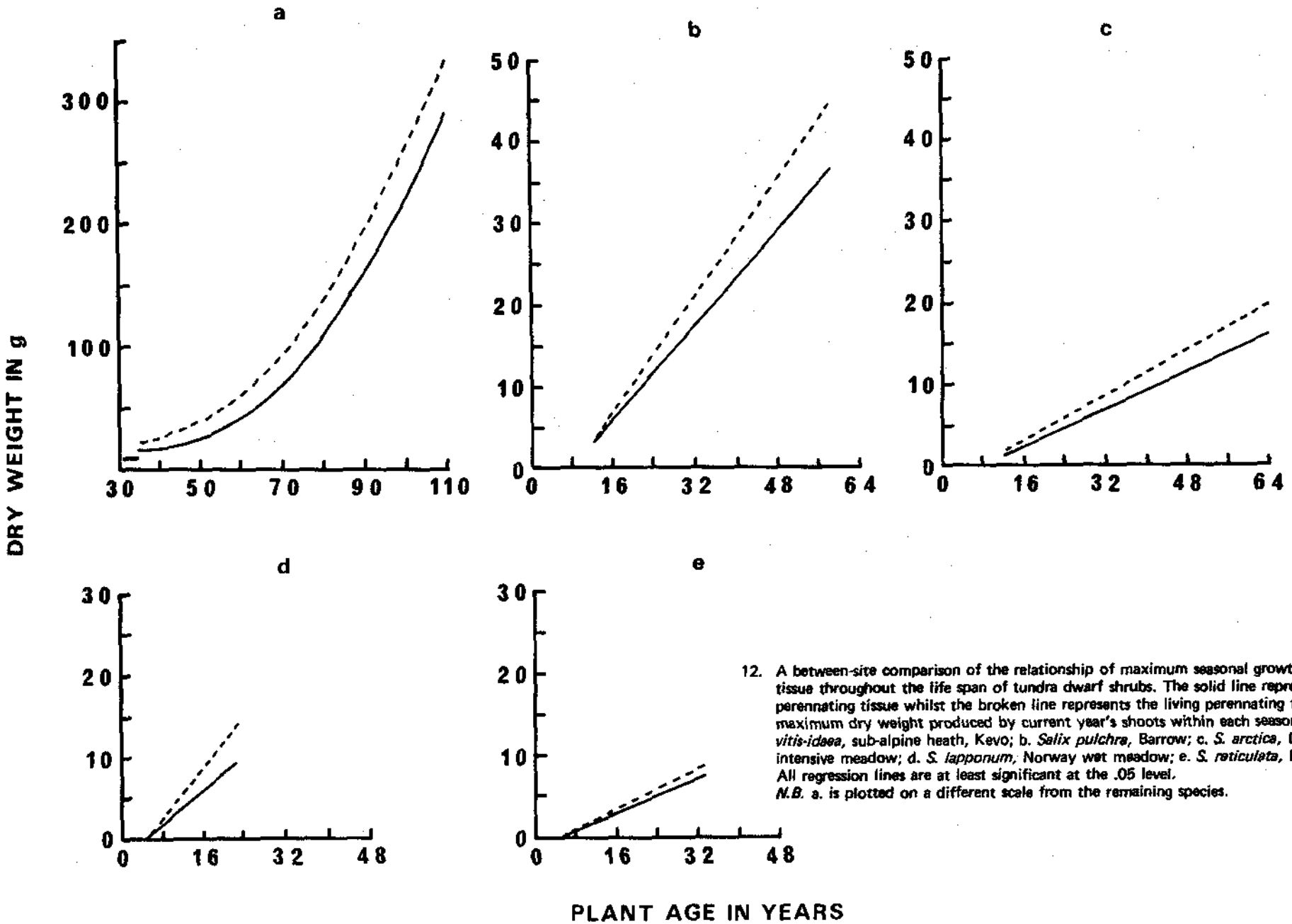
11. A between-site comparison of the increase in number of young shoots with above-ground branch age in a. *Salix glauca* at the Disko Island sites and b. *Myrica gale* at Glenamoy. The broken line represents the number of dead plus living current year's shoots, whilst the bars represent the maximum standard errors. All regression lines are at least significant at the 0.05 level.
N.B. The data are presented on different scales.



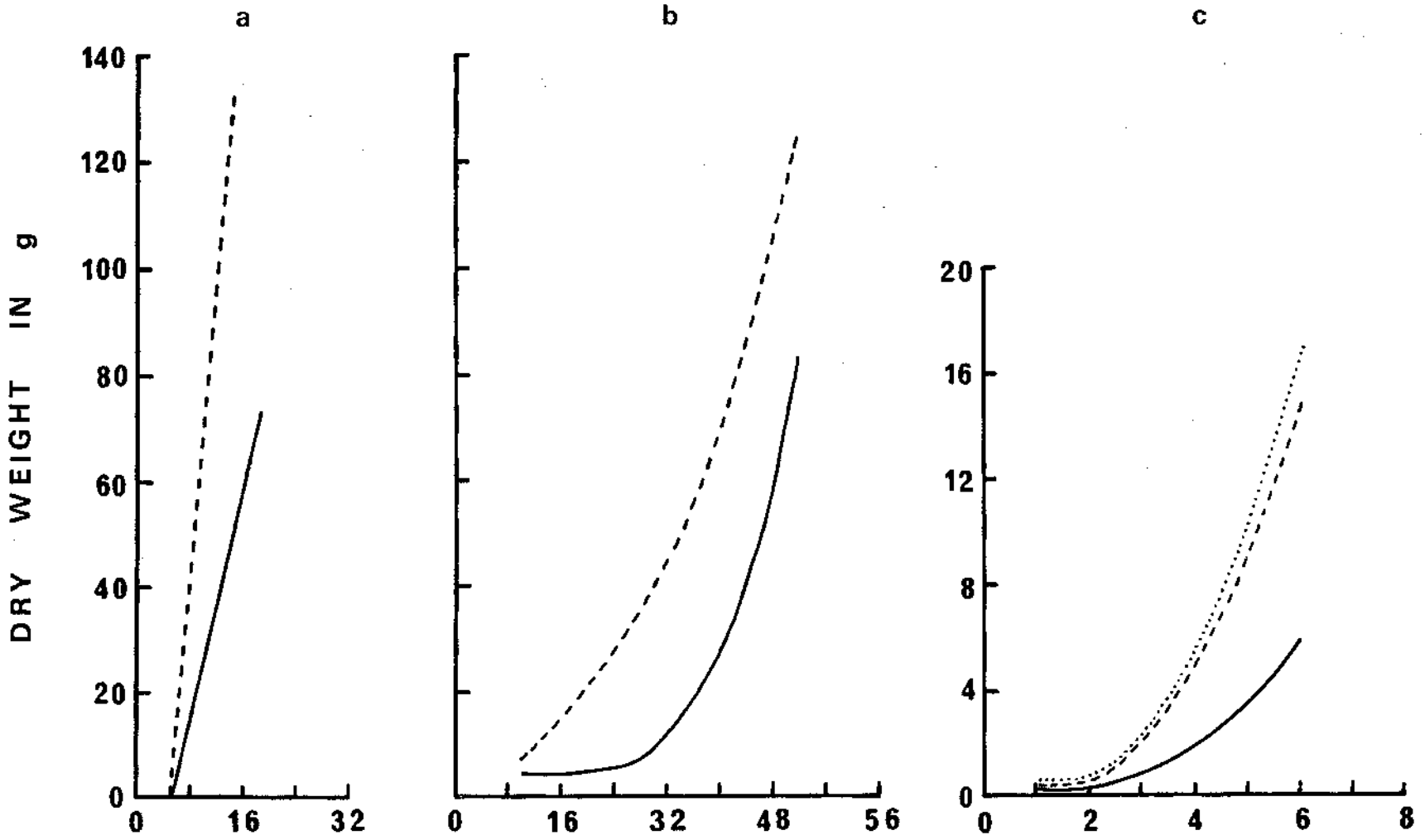
10. A between-site comparison of the increase in number of current year's shoots with age for a. the faster growing species and b. the slower growing species. Bars represent maximum standard errors. All regression lines are at least significant at the .05 level.
N.B. There is a tenfold difference in the vertical scales of a. and b.



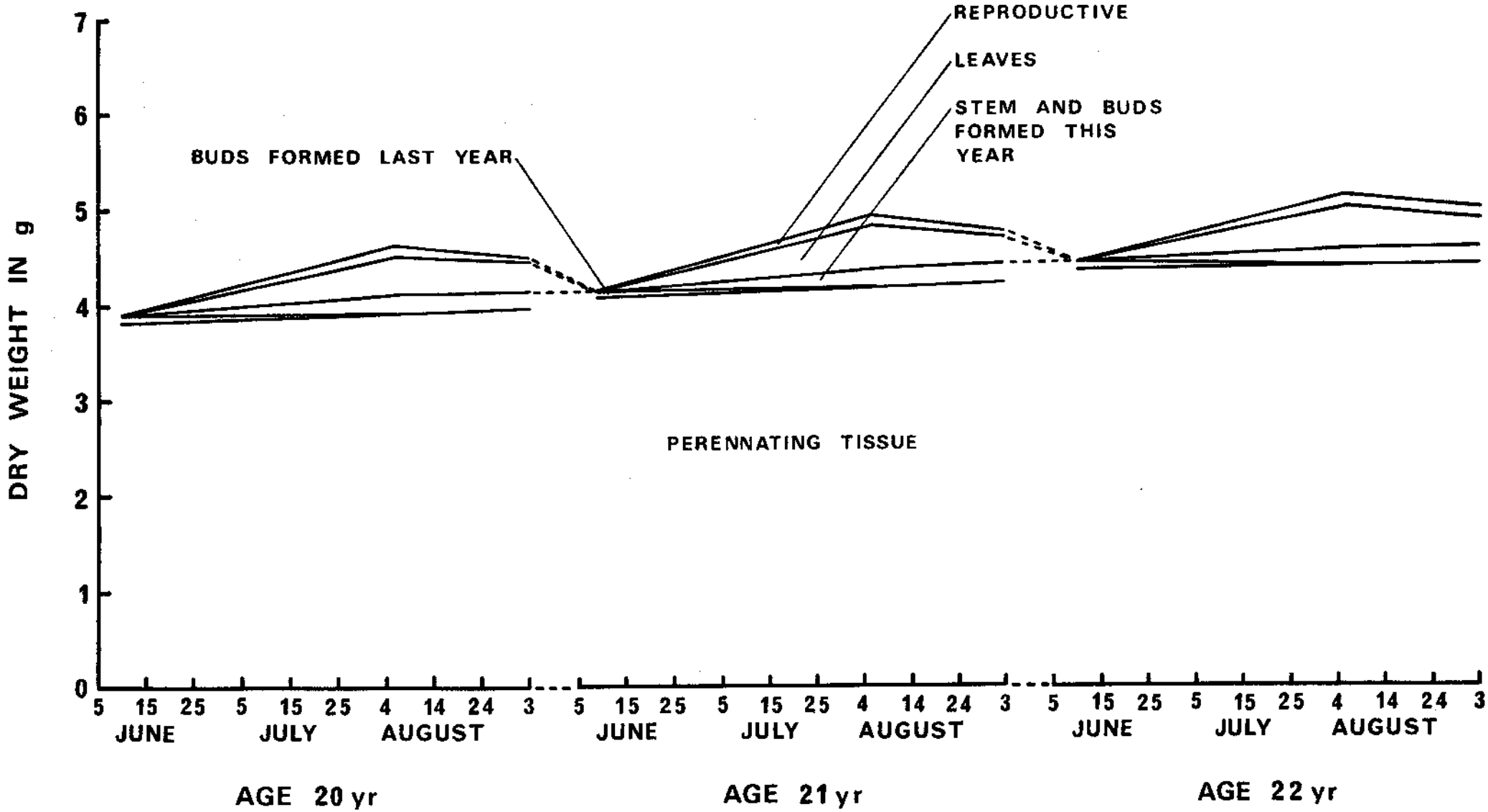
9. A between-type comparison of the increase in dry weight of above-ground perennating tissue (i.e. living wood) and above-ground dead wood (broken lines) in tundra dwarf shrubs. a. *Salix glauca,* Disko Island primary site; b. *S. glauca,* Disko Island fell field; c. *Myrica gale,* Glenamoy. Lower bars represent maximum standard errors of living tissue whilst the upper bars represent the maximum standard errors of living plus dead tissue. All regression lines are at least significant at the .05 level.



12. A between-site comparison of the relationship of maximum seasonal growth to perennating tissue throughout the life span of tundra dwarf shrubs. The solid line represents the living perennating tissue whilst the broken line represents the living perennating tissue plus the maximum dry weight produced by current year's shoots within each season. a. *Vaccinium vitis-idaea*, sub-alpine heath, Kevo; b. *Salix pulchra*, Barrow; c. *S. arctica*, Devon Island, intensive meadow; d. *S. lapponum*, Norway wet meadow; e. *S. reticulata*, Norway dry meadow. All regression lines are at least significant at the .05 level.
N.B. a. is plotted on a different scale from the remaining species.



13. A between-site comparison of the relationship of maximum seasonal growth to above-ground perennating tissue in tundra dwarf shrubs. The solid line represents the living above-ground perennating tissue whilst the broken line represents this plus the maximum dry weight produced by young shoots within each season. The dotted line in c. represents the dead current year's tissue added cumulatively. a. *Salix glauca,* Disko Island primary site; b. *S. glauca,* Disko Island fell field; c. *Myrica gale,* Glenamoy. All regression lines are at least significant at the .05 level. *N.B.* The data are plotted on different scales.



14. The growth of *Salix reticulata* from the dry meadow Norway, over three years of its life. The relationship of the assimilatory, reproductive and structural tissues produced within each season to the slowly increasing perennating tissue is shown. The transition of current year's stem into perennating tissue can also be seen.